The effect of habitat creation for predatory arthropods on aphid populations in winter wheat

Thesis

THE EFFECT OF HABITAT CREATION FOR PREDATORY ARTHROPODS ON APHID POPULATIONS IN WINTER WHEAT

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A thesis submitted in partial fulfillment of the requirements of The Open University for the degree of Doctor of Philosophy

Discipline: Agriculture / Environment

MAY 1999

Harper Adams University College

Sponsoring establishment:
Collaborating Establishment:
Allerton Research and Educational Trust
Leicestershire

DATE OF AWARD: 13 SEPTEMBER 1999

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789 East Eisenhower Parkway
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ABSTRACT

Data are presented from research conducted to investigate the role of beetle banks in the biological control of cereal aphids.

A project designed to compare overwintering predator densities in a newly established beetle bank and two conventional hedgebanks over a five year period, indicated that predator densities were similar to or greater than those in the surrounding hedgebanks by the second year of the beetle banks establishment. Predators found overwintering on the beetle bank included many species that are considered to be important predators of cereal aphids. A further overwintering experiment conducted over a four year period, investigated five different grass species sown on beetle banks and a natural regeneration treatment, for their suitability in providing overwintering cover for polyphagous predators. Overall, the highest overwintering predator densities were recorded in grass species with tussocky growth forms and the lowest predator densities were recorded in treatments where the vegetation on the beetle bank had been allowed to naturally regenerate.

During the spring and summer, a predator exclusion experiment was conducted to explore the effect of polyphagous predators emigrating from a beetle bank on cereal aphid populations in an adjacent crop of winter wheat. The results from this experiment indicated that polyphagous predators significantly reduced aphid populations in the crop, though the impact of polyphagous predation appeared to decrease with increasing distance away from the beetle bank. The results from the exclusion experiment, together with the results from a further experiment investigating the effect of the presence or absence of a beetle bank on the distribution of polyphagous predators in crops, also indicated that beetle banks aid the rapid colonisation of cereal fields by polyphagous predators in the early spring, when the potential for aphid control is optimal.

Cost-benefit analysis suggested that an aphid population kept below spray threshold levels by enhanced natural enemy populations emigrating from a beetle bank, could result in a small but potentially useful saving in insecticide costs. The results are discussed in the context of current agricultural policies and in relation to the potential environmental benefits of reducing the reliance upon chemical methods to control cereal aphids. Further research needs are also identified.

ACKNOWLEDGEMENTS

I would like to acknowledge the help and support of my supervisors Dr A Wilcox and Dr K Chaney at Harper Adams University College and Dr N Boatman at the Allerton Research and Educational Trust. I would also like to thank Dr J Holland at the Game Conservancy Trust for his advice throughout this research. This work was funded by the Ministry of Agriculture, Fisheries and Food.

In addition, I acknowledge Jenny Atkinson and Joanna Wilmott for assisting in the running of field experiments and I acknowledge Mr J Daws for helping to identifying Araneae collected during this investigation. I would also like to thank the farm staff at the Allerton Research and Educational Trust, Parkers Ltd and the Edmonthorpe Estate for accommodating my experiments.

Finally, I would like to thank all my colleagues at Harper Adams and my family, especially Garth, for their support and encouragement throughout this research.

PUBLICATIONS

Collins K L, Wilcox A, Chaney K and Boatman N D (1996) Relationships between polyphagous predator density and overwintering habitat within arable field margins and beetle banks. Brighton Crop Protection Conference 2: 635-640

Collins K L, Wilcox A, Chaney K, Boatman N D and Holland J M (1997) The influence of beetle banks on aphid population predation in winter wheat. Aspects of Applied Biology 50: 341-346

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CHAPTER 1.

INTRODUCTION AND LITERATURE REVIEW

1.1 INTRODUCTION

Cereal aphids cause direct damage to cereal crops, resulting in reduced yields and grain quality (Wratten, 1975; Lee *et al.*, 1981; Oakley *et al.*, 1993; Oakley & Walters, 1994). Experimental evidence has indicated that many polyphagous arthropod predators commonly found in cereal fields, have the potential to control aphid population growth, thus reducing economic losses (Edwards *et al.*, 1979; Sunderland & Vickerman, 1980; Sunderland *et al.*, 1987; Chiverton, 1986). However, intensive farming methods have had a detrimental impact on polyphagous arthropod predators found in arable landscapes (Vickerman & Sunderland, 1977; Aebischer, 1991; Asteraki *et al.*, 1992; Greig-Smith *et al.*, 1992; Purvis & Bannon, 1992; Çilgi *et al.*, 1993). It has been suggested that by augmenting polyphagous predator numbers in cereal crops via the creation of mid-field overwintering habitats, aphid populations may be controlled and reliance upon chemical control methods can be reduced (Thomas, 1991). These mid-field overwintering habitats are now generally referred to as beetle banks. The role of beetle banks in the biological control of cereal aphids has not been substantiated and is therefore the subject of this thesis.

This chapter discusses the ecology of polyphagous arthropod predators in the context of their role as predators of aphids in cereal crops. The detrimental impacts of intensive farming practices on polyphagous predators are also reviewed and ways to augment predators in arable landscapes to control aphids, thus potentially reducing the reliance upon chemical control methods are discussed.

1.2 POLYPHAGOUS ARTHROPOD PREDATORS AND THEIR POTENTIAL FOR USE AS BIOLOGICAL CONTROL AGENTS AGAINST CEREAL APHIDS ON WINTER WHEAT

Polyphagous arthropod predators, as their name suggests, feed on a wide variety of prey items. In arable ecosystems their prey includes pest species such as cereal aphids. Polyphagous predators that have been shown to play a role in aphid suppression are represented predominantly within the Carabidae, Staphylinidae and Araneae. The role of polyphagous predators in the biological control of cereal aphids is discussed here.

1.2.1 The importance of aphids as pests of winter wheat

Aphids damage cereal crops directly during the summer via the removal of nutrients from the plant, and also indirectly in the autumn by the transmission of viruses such as Barley Yellow Dwarf Virus (BYDV). Both of these processes lead to a reduction in yield and quality of the grain produced. Two species of aphid are mainly responsible for causing direct damage to winter wheat in the UK; these are *Sitobion avenae* and *Metopolophium dirhodum* (english names where applicable and authorities of all the flora and fauna mentioned in the thesis are given in Appendix I). *Rhopalosiphum padi* on the other hand plays a major role in the transmission of BYDV (Gratwick, 1992).

This study is mainly concerned with the direct damage caused to winter wheat by *S. avenae* during the spring and summer when polyphagous predators are abundant. Less is known about the predator fauna in cereal fields during the autumn when BYDV is mainly transmitted. All the stages in the life cycle of *S. avenae* are spent on grasses and cereals. Viviparae of this species often overwinter on autumn sown cereals and are therefore already present in the crop by spring (Carter *et al.*, 1982). However populations of *S. avenae* rarely become numerous until late June (Gratwick, 1992). The majority of research conducted within the UK has focused on the detrimental effects of *S. avenae* as opposed to *M. dirhodum*. This is partly because *S. avenae* is the species that most frequently causes direct damage to winter wheat in the UK, with *M. dirhodum* reaching damaging levels only sporadically (Dent, 1995). Small numbers of *S. avenae* also have a greater impact on yield compared to *M. dirhodum* because *S. avenae* removes nutrients directly from the grain (Holmes, 1984), thereby affecting grain quality, through the removal of high molecular weight glutenins which are important in bread making (Lee *et al.*, 1981). Yield loss is further increased by a reduction in the flag leaf's photosynthetic area which reduces assimilate supply to the ear (Wratten, 1975). This is brought about by the fungal colonisation of honeydew excreted by aphids (mainly *M. dirhodum*) on the leaf surface (Drenth *et al.*, 1989).

During the late 1970s the recommended economic threshold for spraying wheat infested with *S. avenae* was set at 'five or more aphids per ear and the population increasing at the beginning of flowering' (George & Gair, 1979). However more recent research has led The Agricultural Development Advisory Service (ADAS) to recommend that spray

applications should be applied when 'two-thirds of the total number of ears in the field have one or more *S. avenae* on them at the beginning of flowering' (Oakley & Walters, 1994). Although spraying at the flowering stage can prevent a potential yield loss of up to 20% (Gratwick, 1992), many insecticides also have a detrimental effect on non-target organisms such as polyphagous predators (Vickerman & Sunderland, 1977; Greig-Smith *et al.*, 1992; Çilgi *et al.*, 1993). Evidence cited later in this thesis indicates that a reduction in predators within cereal fields can lead to an increase in pest problems and thus an increase in input costs (ie. pesticides) for farmers. Therefore, ways in which predators can be augmented within cereal fields to naturally control aphid populations, warrant further investigation and are the subject of this thesis.

1.2.2. Experimental evidence for the suppression of aphid population growth by polyphagous predators

Potts and Vickerman (1974), were amongst the first researchers to suggest that polyphagous arthropods were partly responsible for the natural control of aphid populations within cereal crops in the UK. Around the same time workers such as Sunderland (1975), reported that several species of polyphagous predator collected in cereal fields had the remains of aphids in their gut. Although these workers hypothesised that polyphagous predation in the pre-peak period of aphid population growth, was probably the most important factor in preventing the build up of an aphid population, there was little field evidence to support this theory. Edwards *et al.* (1979) manipulated populations of polyphagous predators in winter wheat fields to examine the impact of early and late polyphagous predation on cereal aphid populations. Using predator-exclusion barriers which prevent the ingress of ground dwelling predators into plots of wheat, they found that peak aphid populations were greater in plots where polyphagous predators had been reduced in early spring (March & April), before aphid populations had time to establish. An inverse correlation was also recorded between polyphagous predator and aphid densities, in contrast to a positive relationship observed between aphid-specific predator and parasitic 'mummy' densities with aphid densities. Consequently, these pieces of evidence led Edwards *et al.* (1979) to conclude that predation by polyphagous predators in the aphid pre-peak phase, is important if aphid populations are to be prevented from reaching recommended spraying thresholds later in the season. Chiverton (1986) provided further conformation of the results found by Edwards *et al.* (1979). By reducing

polyphagous predator populations (again using barriers) in the pre-peak period of the aphid *R. padi*, he found that peak aphid populations were two to six times higher where polyphagous predation had been reduced.

However manipulative experiments such as these, do not readily identify which polyphagous predator species are actually responsible for prey reduction. Results also have to be interpreted carefully, as other predator groups not excluded by the barriers ie. aphid-specific predators may also have had an impact on the aphid populations. Edwards *et al.* (1979) and Chiverton (1986) made some assumptions about the relationship between certain predator species and aphid density, which were based on the abundance of these predators over a particular time period and their known feeding biology. Two carabids highlighted as having strong inverse relationships with aphid density were *Agonum dorsale* (Edwards *et al.*, 1979) and *Bembidion quadrimaculatum* (Chiverton, 1986). These two studies mainly concentrated on the relationship between carabid and aphid densities, providing little information for other polyphagous predators such as the Staphylinidae and Araneae.

1.2.3 The suppression of aphid populations by individual species and 'guilds' of polyphagous predators

Sunderland and Vickerman (1980), studied the potential importance of twenty species of polyphagous predator in relation to aphid density, by examining the gut contents of c. 12000 individuals caught in cereal fields between 1972-1977. Each species was assigned to a predation index (proportion containing aphid remains during the aphid increase phase multiplied by the mean density of the predator at that time), whereby high predation indices implied greater predation at lower aphid densities. Two carabid species were highlighted as having particularly high predation indices: *Agonum dorsale* and *Demetrias atricapillus*. However, the importance of staphylinid species was thought to be underestimated in this study because many of the species belonging to this family are fluid feeders and therefore solid aphid remains would not be found in the guts of these invertebrates.

To overcome this problem Crook and Sunderland (1984) developed a double antibody sandwich enzyme-linked immunosorbant assay (ELISA), for detecting the presence of

aphid antigens in predators. Sunderland *et al.* (1987a) used this technique along with gut dissections, to obtain predation indices particularly for fluid feeding species so that they could be compared to findings for other predators that ingest whole aphids. This work revealed that the value of some predators in biological control had been vastly underestimated. For example out of 105 species tested (both fluid feeders and those that ingest whole aphids), the linyphiid spiders *Erigone atra* and *Erigone dentipalpis* had the highest predation indices at the lowest aphid densities before flowering occurred. These two species, therefore, have the potential to play a vital role in the prevention of aphid populations reaching recommended spraying thresholds.

Spiders also contribute to the biological control of cereal aphids in rather a different way. Sunderland *et al.* (1986), found that linyphiid webs can cover more than 50% of a field by late July, and that small aphids falling into these webs are unlikely to escape, even if the spider is satiated or absent. They also reported that although web cover is lower during spring, approximately 16% of *S. avenae* are estimated to encounter webs, with the timing thought to be early enough to be of economic importance ie. preventing aphid populations reaching recommended spray thresholds.

Limited work has been performed using single species in exclusion experiments as these studies are very time consuming, however one such study was carried out by Dennis and Wratten (1991). These workers investigated three adult species of staphylinids namely *Tachyporus obtusus*, *Tachyporus chrysomelinus* and *Philonthus cognatus*, for their effect on the population development of *S. avenae*. A novel cage design was used to cage each species separately on winter wheat, excluding all other predators except for the species under investigation. The results showed that *T. obtusus* and *T. chrysomelinus* can reduce the numbers of *S. avenae* prior to the exponential phase of aphid population increase, whilst *P. cognatus* causes some reduction at both high and low aphid densities.

ELISA testing and gut dissection, do not distinguish between dead aphids that have been scavenged by predators or the consumption of live aphids. Predation indices based on results using these methods may therefore underestimate the true impact of predator guilds (ie. a group of species exploiting the same resource in a similar fashion (Root, 1967)), such as ground and climbing predators, on aphid populations, as only aphids which are consumed alive result in a reduction of a developing aphid population. Many predator

species that have been ranked highly as cereal aphid predators, such as *Agonum dorsale*, rarely climb wheat plants to reach live aphids on the ear and flag leaves (Griffiths *et al.*, 1985). The potential for ground predators to control aphids will therefore largely be determined by the proportion of live aphid populations arriving on the ground and their fate in the absence of predation (Griffiths *et al.*, 1985).

Sopp *et al.* (1987) showed that the proportion of aphids found on the ground was greater when low densities of aphids were observed on wheat plants compared to high densities (eg. 18% on the ground at 100 aphids m^{-2} on plants and 4% at 2500 aphids m^{-2}). They concluded that a high proportion of aphids on the ground during the pre-peak phase could explain the early season predation peaks observed for many polyphagous predators in cereals. However, observations indicated that around 30% of the aphids found on the soil were dead. This work contradicts that found by other researchers who found that the proportion of aphids on the ground increases with increasing aphid density on wheat plants (Griffiths *et al.*, 1985; Sunderland *et al.*, 1986). These differences may be attributed to the multitude of factors that affect the movements of aphids between cereal plants and the ground. For example rain and wind knocking aphids off the ears and leaves (Mann *et al.*, 1995), and predator disturbance which has been found to cause aphids to fall from plants (Losey & Denno, 1998). Winder *et al.* (1994) incorporated both field and laboratory data into a model to compare the potential availability of live aphids to climbing and ground predators. They concluded that most of the aphids that fall to the ground are alive and that climbing predators contact more live aphids than ground predators because the availability of aphids to predators on the ground was low, as aphids quickly returned to the crop canopy (5-7 minutes). This model however assumed that ground predators forage randomly and therefore more time would be spent on searching for prey rather than consuming it. Bryan and Wratten (1984) found that some ground dwelling Carabidae show an aggregative response to patches of high aphid density (eg. *Agonum dorsale* and *Amara plebeja*), and therefore the time budget of the predator may be reversed, with longer periods of time spent consuming live aphids that have fallen to the ground. Halsall and Wratten (1988) also found similar results with the carabid *Bembidion lampros*, which preferentially feeds on live aphids and occurs at high densities in cereal crops. Further research is therefore needed to fully understand the role of polyphagous ground predators on aphid population control. However without ground predation a proportion (which may

be significant) of those aphids that do fall to the ground will be able to return to the crop canopy and reproduce.

1.3 ENHANCEMENT OF PREDATOR COMMUNITIES ON FARMLAND VIA HABITAT CREATION

In temperate zones many invertebrates adapt to adverse weather conditions during winter months by entering diapause. Whilst in diapause the invertebrates' metabolic rate slows down to conserve energy until more suitable conditions prevail (Foelix, 1982). To enhance their survival during this time, invertebrates locate a suitable overwintering habitat which will afford some protection against detrimental abiotic conditions such as the cold and flooding.

Those species of polyphagous predator which have been ranked highly as cereal aphid predators by Sunderland and Vickerman (1980) overwinter almost exclusively in field boundaries, they do not overwinter in grassland, winter-sown cereals, cereal stubbles or woodland (Sotherton, 1984). For example, these species include *Demetrias atricapillus*, *Agonum dorsale*, *Tachyporus chrysomelinus*, *Tachyporus hypnorum*, *Bembidion lampros*, *Amara familiaris* and *Amara plebeja*. Sotherton (1985) found that field boundaries in the form of raised banks with tussocky grass cover, such as hedgebanks, supported the highest densities of overwintering polyphagous predators. Tussocky grass species (eg. *Dactylis glomerata*), have long been associated with supporting high densities of overwintering polyphagous predators (Luff, 1966). This relationship is thought to result from the microclimatic conditions found within tussocks during winter months. Several workers have shown that although temperatures within tussocks are low during winter, they are more stable compared to those found in grasses with loose growth forms (Brossenbroek *et al.*, 1977; Luff, 1966; Thomas *et al.*, 1992a). This is thought to enhance overwintering survival of predators and may act as an abiotic cue in overwintering site selection (Thomas *et al.*, 1992a).

During the past 50 years, arable landscapes have changed dramatically to adapt to more intensive farming methods, for example the removal of hedgerows to create larger fields. A net loss of 24,600 kilometres of hedgerows was recorded between the years 1977/78 and

1984 (Anon, 1986). Between 1984 and 1990 the rate of hedgerow removal was even higher (Barr *et al.*, 1991). The incidence of spraying herbicide to control weeds in hedgerows has also increased (Boatman, 1989), which along with the inaccurate placement of inorganic fertilisers has led to the replacement of diverse grass cover in many modern field boundaries by aggressive annuals such as *Galium aparine*. These species not only provide poor overwintering cover for invertebrates, but also pose an agronomic problem to farmers (Sotherton, 1995). These farming practices have therefore resulted in a loss of overwintering habitat for predators, as those field boundaries that still exist are often of reduced quality and do not provide the ideal overwintering habitat for polyphagous predators. The creation of larger fields for arable production has also had two further detrimental consequences in terms of the control of aphid populations by polyphagous predators. Firstly, large fields have a small boundary:field area ratio and therefore the final density of predators in the crop originating from boundary habitats could be lower than that in smaller fields (Thomas *et al.*, 1991). Secondly, in large fields predators that disperse by walking may still be in close proximity to field boundaries at the time of an aphid invasion (Coombes & Sotherton, 1986) and aphid populations may therefore develop in field centres in the absence of sufficient polyphagous predation.

Although many Carabidae disperse by flying, dispersal is dominated by walking in cereal fields (Coombes & Sotherton, 1986; Wallin & Ekbom, 1988; Thomas *et al.*, 1998). Some carabid species can potentially cover large distances in one day by walking. For example, Wallin and Ekbom, (1988) recorded velocities of 2.4m/hr and 3m/hr respectively for the open-field inhabiting *Pterostichus melanarius* and *Harpalus rufipes* in cereal fields. However, Coombes and Sotherton (1986) showed that carabid species which have been ranked highly as cereal aphid predators disperse in a slow wave from boundary habitats into the crop during spring. Complete dispersal of *Demetrias atricapillus* and *Bembidion lampros* over a distance of 100m took approximately 50 days and 30-40 days respectively. Conversely these workers showed that the staphylinids *Tachyporus hypnorum* and *Tachyporus chrysomelinus* exhibited a rapid rate of dispersal which was complete by mid-April, when the Carabidae were only first appearing in traps close to field boundaries. Aphid distributions are usually non-random in fields and are higher in the middle of fields during May/June than at field edges (Chambers *et al.* 1982; Coombes & Sotherton, 1986). Coombes and Sotherton (1986) showed that *Demetrias atricapillus* and another carabid *Agonum dorsale*, did not complete dispersal over distances of 100m to 200m into the crop

until early June. Therefore populations of these carabids may not be in sufficient numbers at field centres, particularly in large fields, at a time when aphid populations are slowly increasing.

Studies investigating the re-colonisation of polyphagous predators into areas treated with pesticides, have also confirmed that carabid dispersal is slower compared to that by other polyphagous families. Duffield and Aebischer (1994) showed that after applications of dimethoate, re-invasion by new individuals into the treated area was fastest by the Staphylinidae and Linyphiidae and slowest by the Carabidae. Many Staphylinidae in the UK disperse by flight (Good & Giller, 1988) and Linyphiidae disperse mainly by a process known as ballooning (Roberts, 1995). By these processes species belonging to these two families can disperse over large distances in a short space of time. For example under the right weather conditions linyphiids can be redistributed from a field over a range of 1 Km to 6 Km downwind in a single day (Thomas, 1992).

Thomas *et al.* (1991) sought to overcome the above problems by creating artificial overwintering habitats for polyphagous predators on farmland in Hampshire. These habitats took the form of linear grassy ridges situated in the centre of cereal fields, which are now generally referred to as 'beetle banks' (Plate 1). The creation of beetle banks aimed to achieve the following: i) the provision of adequate overwintering cover within arable systems for predators ii) the enhancement of predator densities within cereal fields for biological control and iii) a reduction in field size to enable predators with low powers of dispersal to disperse fully throughout a field before an aphid invasion is likely. Thomas *et al.* (1991) incorporated those features of good quality field boundaries found by Sotherton (1985) to support high densities of overwintering predators, into these habitats. For example, a raised bank was chosen because the soil is less likely to reach water saturation point due to better drainage and thus predators are less prone to being frozen during winter months (Sotherton, 1995). These workers also investigated a range of grass species which could be sown on beetle banks to provide overwintering cover for predators. These were *Dactylis glomerata*, *Holcus lanatus*, *Agrostis stolonifera* and *Lolium perenne*. *D. glomerata* and *H. lanatus* supported the highest densities of polyphagous predators, with densities exceeding those recorded in surrounding good quality field margins. For example, predator density exceeded $1500m^{-2}$ in *D. glomerata* treatments in the second year

Plate 1. A beetle bank (right hand side of picture) on the Loddington Estate, Leicestershire

of the grasses' establishment compared to $1000m^{-2}$ in existing good quality field boundaries.

Preliminary work on the potential benefits of beetle banks for biological control by Thomas *et al.* (1991) indicated that a wave of predator emigration from the bank into the crop did occur during the spring as expected. However the optimum distance between beetle banks in large cereal fields in order to maximise predator dispersal still remains to be answered. Thomas (1989) also investigated the effect of early season predation of artificial prey items by predators emigrating from a beetle bank. Predation was assessed by placing prey items both on the beetle bank and at various distances leading into the adjacent crop from the beetle bank. He found that predation of prey items was greatest on the beetle bank itself and its immediate environment. However, because of the design of the experiment ie. placing dead prey in petri dishes along a transect, the impact of predation by fluid feeding predators such as the Staphyinidae and predators that only take live prey such as the Araneae was not assessed. Damage caused to the prey by small mammals also confounded the results obtained.

The high predator densities recorded on beetle banks in Hampshire led The Game Conservancy Trust to promote 'beetle banks' to farmers, by producing an explanatory leaflet explaining how to create beetle banks. More recently beetle banks have been included in the options offered by The Countryside Stewardship Scheme, from which farmers can obtain grants of £15/100m/year, for creating beetle banks on their land (MAFF, 1996 & 1999a). However the role of beetle banks in agroecosystems has yet to be substantiated, for example there is no evidence that beetle banks actually augment predator densities within cereal fields, as the 'enhanced' densities may simply be a consequence of redistributing existing predator populations (Thomas *et al.*, 1991). Furthermore there is little evidence that 'enhanced' predator populations resulting from beetle banks can control aphid population growth. This thesis will attempt to provide some insight into these questions.

1.3.1 Cost and construction of beetle banks

Beetle banks are created by two directional ploughing, preferably during the autumn. They should reach a height of approximately 0.4m high and a width of 2m. Length is dependant

upon field size, but a gap of at least 25m should be left at either end to prevent hindrance to farm machinery and allow the field to continue being worked as a single unit (Sotherton, 1995). Grass cover for example by *D. glomerata*, is established following hand sowing, either when the ridge is newly formed or in the following spring (Sotherton, 1995). Flowering plants, for example members of the Umbelliferae (Jervis *et al.*, 1993) can also be sown on beetle banks to provide pollen and nectar during the summer months, for aphid-specific predators such as Syriphidae and parasitic wasps.

Thomas *et al.* (1991) quoted the cost of establishing a beetle bank at c. £85 in the first year for a 20-ha winter wheat field. This included the combination of labour costs for bank establishment, yield loss due to land being taken out of production and the cost of grass seed. Subsequent costs would comprise gross yield loss at only £30 per year. However, these figures have changed since 1991 and will be reassessed within this thesis.

1.3.2 Alternative techniques for enhancing predator and reducing pest populations on farmland.

Examples of other techniques that have been shown to enhance predator populations on farmland include, increasing the intra-crop diversity (Dempster, 1969; Powell *et al.*, 1985; Parajulee *et al.*, 1997) and the creation of new non-crop habitats other than beetle banks around or within fields (Nentwig, 1988 & 1989; Lys & Nentwig, 1992; Frank & Nentwig, 1995; Hawthorne & Hassall, 1994 & 1995; White & Hassall, 1994; Frank, 1997; Baines *et al.*, 1998). Some of these techniques have also been found to reduce pest numbers in the crop (Parajulee *et al.*, 1997).

It is now well documented that increasing plant diversity in crops can enhance populations of beneficial predators. This has mainly been achieved by intercropping and retaining weed flora in crops. Intercropping is 'the cultivation of two or more species of crop in such a way that they interact agronomically' (Vandermeer, 1989). This can be achieved by i) undersowing when an economically important main crop is undersown with an intercrop which has no economic significance, but is used to diversify the agro-ecosystem or to influence the main crop ii) mixed crop where all the components have a market value (Theunissen, 1997). Undersowing and retaining weed flora are thought to enhance predator numbers because these techniques increase shelter and humidity in the crop

which aids the survival of adult and larval predators which are prone to desiccation in hot summers (Powell *et al.*, 1985). A greater abundance of prey is also encouraged using these techniques and Speight and Lawton (1976) showed that removal of artificial prey was greatest where weed cover was increased in winter wheat. However although higher prey densities may encourage predators to remain in the crop when aphid densities are low, prolonged availability of alternative prey may reduce predation pressure on aphids (Powell *et al.*, 1985; Chiverton & Sotherton, 1991). Pest density may not necessarily be reduced in strip intercropping either (Bugg *et al.* 1991). Strip intercropping is where two or more crops are grown simultaneously in different strips. Here the intercrop may act as a sink for predators by being more attractive than the primary crop itself (Parajulee *et al.*, 1997).

Undersowing and weed retention have also been shown to hinder the activity of *Pterostichus melanarius* and other large carabids (Greenslade, 1964; Dempster, 1969), though not smaller carabids such as *Agonum dorsale* (Powell *et al.*, 1985). Armstrong and McKinlay (1997a & 1997b) also found that carabid species differ in their response to plant cover in crops. This may have important consequences for biological control, as some species which may be important predators of a particular pest, may be deterred from crops by the presence of dense vegetation.

Parajulee *et al.* (1997) showed that relay intercropping as opposed to strip intercropping increased the abundance and early arrival of predators in cotton and reduced cotton aphid numbers. Relay intercropping involves growing two or more crops simultaneously during part of the life cycle of each (Vandermeer, 1989). This results in less competition between crops for resources and the relay crop provides a predator reservoir that is in place before the arrival of key pests in the primary crop. Depending on the crops chosen they may relay insect predators, without relaying pests, from one crop to the other as each crop matures and senesseces (Parajulee *et al.*, 1997).

The ecological mechanisms underlying the reduction in pest numbers in more diverse crops were investigated by Root (1973), who proposed two hypotheses i) the natural enemy hypothesis in which predators and parasites are more effective in diverse systems and ii) the resource concentration hypothesis where specalist herbivores more easily find and utilise simple systems ie. monocultures. Evidence to support the two theories have been well documented (Risch, 1981; Risch *et al.*, 1983; Redfearn & Pimm, 1987;

Baliddawa, 1985). However later reviews suggested that the two hypotheses are not mutually exclusive of each other (Andow, 1991) and the natural enemy hypothesis was more important than first thought (Wratten & Van Emden, 1995).

Practices such as intercropping and retaining weed flora in crops change the agronomy of the whole field (Wratten & VanEmden, 1995) and the economic value of pest reduction may be potentially offset by competition among crops/plant species and a reduction in mechanisation of the farming system (Van Driesche & Bellows, 1996). Many farmers also have a strong psychological attitude against retaining 'weeds' in crops. Although these techniques have been shown to increase predator populations in crops during summer, the provision of an overwintering resource may be a key factor (Varley & Gradwell, 1960) in the life cycle of many of these predators. If beetle banks were used in combination with these techniques, despite the above problems associated with these practices, then predator populations may be further enhanced on farmland.

Rather than manipulating the intra-crop environment several workers have examined the effect of creating new non-cropped habitats around or within fields. Nentwig (1988 & 1989; Lys & Nentwig, 1992) investigated the effects of strip-management on arthropods in farmland, by alternating 1m wide strips of naturally occurring successional vegetation with 12m wide strips of meadowland or winter wheat. He found high densities of arthropods overwintering in the successional strips, which migrated into the wheat strips during spring. Several other experiments have also shown that predator populations can be enhanced on farmland using weedy strips or un-cropped 'wildlife strips' (Frank and Nentwig, 1995; Hawthorne & Hassall, 1995; Frank, 1997). However the role of the predators in the dynamics of aphid populations in the crop were not demonstrated by these experiments and the economic value of pest reduction may be offset by reduced yields due to land being taken out of production (particularly with large numbers of strips). These experiments also provided little evidence that the strips could be used to reduce the size of large fields, thus enabling predators that disperse by walking to fully colonise fields before the onset of an aphid invasion. Large numbers of strips will also cause hindrance to farm machinery.

Compared to the above techniques beetle banks may be a more practical solution to predator enhancement and pest control. As mentioned in section 1.2.1 beetle banks are

inexpensive to create and once established are easy to maintain. They do not alter the agronomy of the whole field and the grasses sown on the banks are not invasive species. The creation of beetle banks in the centre of cereal fields should also enable predators that disperse by walking to fully colonise crops before the onset of an aphid invasion. Preliminary evidence has shown a wave of predator emigration and predatory activity away from the beetle banks during spring, however the real benefits of pest reduction have only been speculated on (Thomas,1989; Thomas *et al.*, 1991). Although recommendations on the spacing of beetle banks in cereal fields are vague, Thomas (1991) suggested that one beetle bank would be sufficient to reduce a 40ha field into two blocks of 20ha to enhance biological control. This would mean far less land would be taken out of production compared to the system in Nentwig's (1988 & 1989) experiments. This thesis will investigate the economic value of pest reduction using beetle banks.

1.4 THE DEVELOPMENT OF INTEGRATED FARMING SYSTEMS

Researchers at the Game Conservancy Trust, were amongst the first to highlight the reduction in invertebrate populations within cereal fields in Southern England, over a period of time (1972-1990) when pesticide usage increased. One of the invertebrate groups that decreased in abundance between 1972 and 1989, was polyphagous predators (25-75%) (Aebischer and Potts, 1990; Aebischer, 1991). The early results from this long-term study, stimulated interest in the mid 1970s into the possible detrimental effects on wildlife, of over using chemicals as insurance against crop losses (Greig-Smith, 1992). At the same time The Ministry of Agriculture, Fisheries and Food's Agricultural Development Advisory Service (ADAS) and others were questioning the efficiency and cost-effectiveness of the prophylactic use of pesticides in crop protection (Greig-Smith , 1992).

Vickerman & Sunderland (1977) showed that application of broad-spectrum (ie. not specific to one type of invertebrate pest) organophosphorus insecticides to winter wheat infested by cereal aphids, also had a deleterious effect on populations of non-target predatory arthropods. During the same time period, evidence was also accumulating about the potential role of polyphagous predators in controlling cereal aphid populations (Potts & Vickerman, 1974; Sunderland, 1975; Edwards *et al.*, 1979). It was hypothesised that the widespread use of such insecticides could damage predatory arthropod populations, which could in turn exacerbate cereal aphid problems (Vickerman &

Sunderland, 1977). Concern was also growing about the potential indirect side-effects of intensive pesticide use. For example the depletion of invertebrate prey for farmland birds.

However, many of the studies investigating the impact of pesticides on invertebrates and the environment as a whole, were performed on a small-scale over short periods of time. Evidence for the long-term deleterious effects of pesticides on the environment was lacking. This led MAFF to commission a large-scale experiment to investigate the possible long-term agronomic and environmental effects of pesticides. This study was called The Boxworth Project and was established in 1981 (Greig-Smith *et al.*, 1992). Three approaches to pesticide use were investigated during the study these were: i) 'high-input'/ 'full insurance' prophylactic approach to crop protection, ii) 'lower input'/ 'supervised' approach whereby the need for pesticide treatment was assessed by monitoring pest, weed and disease levels, applying pesticides only when and where they were needed to prevent economic loss and iii) 'integrated' approach whereby modifications to modern cropping, husbandry and pest control methods, were used in conjunction with a reduction in pesticide use.

One of the aims of The Boxworth Project was to investigate the long-term effects of these pesticide regimes on beneficial invertebrates inhabiting winter wheat fields. The study found that insecticides and molluscicides had a more profound effect on predatory invertebrate numbers compared to herbicides or fungicides. The former were divided into summer applications (pirimicarb) and autumn and winter applications (methiocarb, pyrethroids, chlorpyrifos and triazophos). Overall the total numbers of predators found in the 'full insurance' areas were 53% lower than in the supervised and integrated areas. Those predatory invertebrates which were most affected were i) those which spent the whole year in the field rather than emigrating to field boundaries and were thus exposed to pesticide applications throughout their life cycles (eg. the carabid *Bembidion obtusum*) ii) those which inhabited the plant surface during spring and summer (eg. the carabid *Demetrias atricapillus*) compared to those that either inhabited the soil or the soil surface, where the crop canopy afforded some protection against pesticides.

The dispersal ability of individual species determined the speed at which their populations recovered after fields were treated with pesticide. Those species that showed little or no recovery in the 'full insurance' regime, were those that dispersed by walking (eg.

Bembidion obtusum and *Demetrias atricapillus*). There was also evidence during the study that the reduced activity and or the abundance of many predators in the 'full insurance' regime, may have impeded the polyphagous predation of aphids (Burn, 1988 &1992). For example, the rose-grain aphid *Metopolophium dirhodum*, twice (1986 & 1987) reached densities ten times higher in the 'full insurance' area than in the 'supervised' and 'integrated' areas.

On completion of The Boxworth Project in 1988, it was decided not to extend the project in its original format, as the 'full insurance' regime was considered unrepresentative of the then current farming practices because the pesticide inputs were much higher (Holland *et al.*, 1994). Instead the project was extended in a limited form for a further three years, to assess the recovery of arthropod populations from the 'full insurance' regime to a 'supervised' regime. This work showed that even after the intensity of pesticides was reduced, natural enemy numbers increased slowly, indicating that the effects of intensive pesticide use can last for years (Holland *et al.*, 1994).

Two further projects were funded by MAFF in 1990 to investigate whether, the results obtained at Boxworth could be achieved on a wider scale (eg. at other geographical locations under different environmental conditions) and what the economic consequences of reducing key inputs such as pesticides might be. These two projects were named Seeking Conformation About Results At Boxworth (SCARAB) and Towards A Lower Input System Minimising Agrochemicals And Nitrogen (TALISMAN) respectively (MAFF, 1998a).

The SCARAB Project was established on three different sites across the UK and the impacts of two levels of pesticides were assessed over a six year period. The pesticide regimes were i) 'current farm practice' (CFP) which mirrored the practices of a typical, technically competent and financially astute farmer, with pesticides for control of pests, diseases and weeds applied at manufactures' recommended rates ii) 'reduced input approach' (RIA) where no insecticides, molluscicides or nematicides were used and fungicides and herbicides were applied at reduced or full rates only when required to avoid a significant reduction in crop yield or value (MAFF, 1998a). The results from this project indicated that persistent adverse effects like those in the 'full insurance' regime in the Boxworth trial, could occur under conventional 1990s pesticide inputs (Holland *et al.*,

1994). For example temporary elimination of some carabid species such as *Bembidion obtusum* occurred particularly after applications of chlorpyrifos and dimethoate (Çilgi *et al.*, 1993). Although it was mainly the broad-spectrum insecticides such as dimethoate which had the most deleterious impact on predator numbers, synthetic pyrethroid insecticides also resulted in a temporary reduction in spiders (MAFF, 1998a). Within the SCARAB project complete absence of insecticides and low rates of herbicides did lead to reduced profits in some cases (mainly in potato and sugar beet crops). Therefore a more flexible approach to reducing pesticides may be needed to improve profitability (MAFF, 1998a).

However the results of the SCARAB project had their shortcomings. The long-term negative effects of the pesticide regimes were only detected in one of the eight fields and were related to the use of chlorpyrifos and dimethoate in consecutive seasons, which prevented the recovery of some species (Frampton, 1998 unpublished). The effect of the pesticide regimes was most detrimental on Collembola species and negative effects of the conventional regime on arthropod community composition were only detected when these species were included in the analysis (Frampton, 1998 unpublished). Several other studies have shown greater long-term detrimental effects of broad-spectrum pesticides, particularly on spring breeding carabids, that remain in the open-field throughout their life cycle and which are poor dispersers, such as *Bembidion obtusum* (Purvis & Bannon, 1992; Asteraki *et al.*, 1992).

The regimes in the TALISMAN project were: i) 'current commercial practice' (CCP) with nitrogen, fertiliser and pesticides applied to manufactures' or recommended rates and ii) 'a low input approach' (LIA) in which nitrogen rates were applied at 50% below CCP and pesticide applications were omitted or applied at no more than 50% of the rates used in CCP (MAFF, 1998a). In terms of pesticide inputs the LIA regime resulted in an average increase in gross margins of 2% in cereals and 1% in break crops compared to the CCP regime. Therefore farmers could maximise returns from conventional arable cropping by adopting a low-input approach (MAFF, 1998a).

Overall, these projects have particularly highlighted the detrimental effects of broad-spectrum insecticides on invertebrates and the possible side effect of an increased pest problem due to the reduction in predatory arthropod numbers. It has been suggested that

restrictions should be placed on the use of broad spectrum insecticides, which have been found to be consistently harmful to beneficial invertebrates, where selective and less persistent compounds are available (Çilgi *et al.*, 1993). The TALISMAN Project, has also indicated that 'low input' farming may be a more profitable option, if grain prices continue to fall, as inputs are used more efficiently.

This more environmentally aware approach to crop production has been termed 'integrated crop management' (ICM). ICM can be defined as: ' a whole farm policy aiming to provide the basis for efficient and profitable production which is economically viable and environmentally responsible. It integrates beneficial natural processes into modern farming practices using advanced technology and aims to minimise the environmental risks while conserving, enhancing and recreating that which is of environmental importance' (MAFF, 1998b). This will be achieved by combining crop rotations with the targeted use of crop protection chemicals and fertilisers, cultivation choice, variety selection and improved energy efficiency, together with a positive plan for landscape and wildlife features (LEAF, 1997). On a smaller scale, the control of a pest on a certain crop, for example cereal aphids on winter wheat, using a range of methods (eg. biocontrol, crop rotations etc) in order to minimise the use of chemical pesticides is called 'integrated pest management' (IPM) (Coombes and Lisansky, 1993).

Integrated crop and pest management form part of 'integrated farming systems' which aims to integrate all types of farming with ecologically preferred technologies, whilst sustaining production of high quality food and achieving maximum profits. It emphasises a holistic approach to farming whereby agriculture plays a vital role not only in the production of food but also in providing a diverse attractive landscape and encouraging biodiversity, including wildlife conservation (Glen, 1995).

Several other long-term research programmes on integrated farming systems have recently been completed or are currently operating within the UK (eg. LINK Integrated Farming Systems (IFS) and LIFE (Less Intensive Farming and the Environment)). ICM is also being promoted to farmers, advisers, the media etc by the organisation LEAF (Linking Environment and Farming) via demonstration farms. In December 1994, The Integrated Arable Crop Production Alliance (MAFF, 1998b) was formed to co-ordinate the research programmes and advisory work carried out by different organisations within the UK.

An experiment conducted within one of these programmes, the LINK IFS Project, highlighted the need for techniques to be employed by farmers to encourage predatory arthropods on farmland, if they are to be relied upon for cereal aphid control (Holland *et al.*, 1996; Holland & Thomas, 1997a). In the LINK IFS project two farming systems were compared i) 'conventional farm practice' (CFP) which represented an agricultural practice (for the area under investigation) carried out by a technically aware, cost-conscious, risk-adverse farmer and ii) an 'integrated farming system' (IFS) which was based on a cost conscious, environmentally concerned farmer who seeks to use non-agrochemical methods of management, with agrochemicals used only as needed to prevent commercial loss (Ogilvy *et al.*, 1994). Polyphagous predators were manipulated within these two systems using exclusion barriers in winter wheat. In the first year using this approach polyphagous predators failed to prevent an aphid outbreak and there were no significant differences between the two systems or the enclosed and control areas in terms of aphid density. The failure of polyphagous predators to prevent an aphid outbreak was partially attributed to the late infestation and rapid build up of aphid populations outstripping predation (Holland *et al.*, 1996). Holland and Thomas (1997a) repeated this experiment in the summers 1995 and 1996. In 1995 the total number of aphid on the ears and flag leaves differed significantly between the enclosed and control areas, and the Carabidae and Araneae were found to have a negative effect on aphid numbers. During 1996 however no significant differences were found even though the aphid build up was slower than that in 1995. Carabid species diversity and density was generally lower in 1996 and aphid populations arrived late when the activity of polyphagous predators with the exception of the Araneae was reduced. In conclusion only when aphid populations arrive early when polyphagous predators are most active, and build up slowly, may aphid population be prevented from reaching recommended spraying thresholds. The researchers also noted that polyphagous predator populations were greater in the integrated sites in Hampshire compared to other LINK IFS Project sites elsewhere in the UK (Holland & Thomas, 1997a). This was probably due to measures being taken at this site over a number of years to encourage invertebrate food for gamebird chicks, for example Conservation Headlands and well managed field margins (Holland & Thomas, 1997a). This led Holland and Thomas (1997a) to suggest that the control of cereal aphids at other LINK IFS Project sites maybe even less considering the lower abundance of polyphagous predators at these sites. In conclusion they emphasised the need for farmers to encourage predatory arthropods on farmland if they are to be relied upon for pest control.

1.4.1 The role of beetle banks in Integrated Farming Systems

One technique that has been suggested as a method of enhancing polyphagous predator populations within cereal fields for the biological control of aphids is that of beetle banks. Thomas *et al.* (1991) estimated that if enhanced predator populations could prevent aphid populations reaching recommended thresholds for spraying, a total of £300 per year could be saved in labour and pesticide costs for a 20 ha field. Results of experiments described in this thesis will be used to substantiate the contribution of beetle banks to integrated crop management in terms of the biological control of cereal aphids in winter wheat and provide a model cost-benefit analysis of their use.

1.5 EXPERIMENTAL AIMS AND HYPOTHESES

The objectives of the research described in this thesis were to:

I. Evaluate the role of beetle banks as overwintering sites for polyphagous predators. Overwintering polyphagous predator densities were compared between a newly established beetle bank and two well established hedgebanks over a five year period. It was hypothesised that the beetle bank would support densities of overwintering predators similar to those in the hedgebanks over time. Successional changes in both predator and vegetational composition were also expected on the beetle bank over the five year period (Chapter 2).

II. Examine a wide range of commercially available grass species and a natural regeneration treatment, for their suitability in providing overwintering cover for polyphagous predators, based on overwintering polyphagous predator densities (Chapter 2).

III. Assess the impact of predator populations arising from the beetle bank on aphid populations in winter wheat. Exclusion barriers were used to assess the impact of polyphagous predation by ground dwelling predators on the aphid *Sitobion avenae*. It was hypothesised that there would be a wave of predatory activity away from the

beetle bank and aphid populations would be greater in the enclosed areas where polyphagous predators were excluded (Chapter 3).

IV. Determine the effect of the presence or absence of a beetle bank on polyphagous predator distribution in crops. This experiment aimed to provide some insight into how effective beetle banks are in enhancing predator dispersal throughout crops during the spring (Chapter 4).

V. Provide a cost-benefit analysis of beetle banks in cereal aphid control (Chapter 5).

The overall aim of these objectives was to provide greater insight into the role of beetle banks in cereal aphid control, as this has not been substantiated by previous studies conducted on beetle banks.

CHAPTER 2.

OVERWINTERING PREDATOR POPULATION DENSITIES WITHIN BEETLE BANKS IN LEICESTERSHIRE

2.1 INTRODUCTION

Over the past decade there has been a substantial increase in the publicity and interest surrounding Integrated Crop Management (ICM) Systems, incorporated into which is the practice of Integrated Pest Management (IPM). Within arable crops polyphagous predators have been identified as important biological control agents of cereal aphids (Edwards *et al.*, 1979; Sunderland & Vickerman, 1980; Sunderland *et al.*, 1987; Chiverton, 1986; Holland & Thomas, 1997a). However, many of these polyphagous predators, particularly those that have been ranked highly as cereal aphid predators, overwinter almost exclusively in field boundary habitats such as hedgebanks, before migrating into the crop in the spring (Sotherton, 1984 & 1985; Andersen, 1997). During the past 50 years there has been a reduction in both the abundance and quality of these habitats on farmland, which has been attributed to an increase in intensive farming practices. Examples are, the removal of hedgerows to create larger fields and an increase in the spraying of herbicides to control weeds in hedgerows (Boatman, 1989; Barr *et al.*, 1991; Sotherton, 1995). These and other factors (eg. prophylactic spraying of broad-spectrum pesticides) associated with intensive farming systems, have had a detrimental impact on polyphagous predator densities in cereal fields (Vickerman & Sunderland, 1977; Aebischer, 1991; Asteraki *et al.*, 1992; Greig-Smith *et al.*, 1992; Purvis & Bannon, 1992; Çilgi *et al.*, 1993). Therefore if densities of those predators sufficient to provide biological control are to be reached then changes in the modern arable landscape will have to be implemented.

Thomas *et al.* (1991) were amongst the first workers in the UK to attempt augmenting predator densities within cereal fields by creating alternative overwintering habitats for polyphagous predators. By creating overwintering refugia in the centre of cereal fields, they aimed to enhance the biological control potential of polyphagous predators by reducing field size. This is particularly important for providing the chance for predators that disperse by walking from overwintering habitats in spring, to fully colonise cereal fields before the onset or in the early phases of an aphid invasion. These habitats are now referred to as beetle banks.

These workers investigated four different grass species, which could be sown on beetle banks to provide overwintering cover for polyphagous predators; these were: *Dactylis glomerata*, *Holcus lanatus*, *Agrostis stolonifera* and *Lolium perenne*. *Dactylis glomerata*

and *Holcus lanatus* were found to support the highest densities of polyphagous predators, over a three year period starting from when the beetle banks were established.

Documented work on overwintering polyphagous predator densities within beetle banks, has arisen mainly from the above studies carried out in Hampshire. Little information is available from beetle banks elsewhere in the UK, under different environmental conditions such as soil type.

The first experiment in this study, investigated whether the results from the *Dactylis glomerata* and *Holcus lanatus* treatments in Hampshire could be replicated on a beetle bank in Leicestershire, where environmental conditions were different. For example, the soils were of a heavy clay type in Leicestershire as opposed to the chalky well drained soils in Hampshire. Overwintering polyphagous predator densities were monitored from the beetle bank's initial establishment over a five year period and compared to those in two mature hedgebanks within the same field, to allow some insight to be gained as to whether the beetle bank provided an equivalent habitat for overwintering predators.

MacLeod (1994) continued the study by Thomas *et al.* (1991) in Hampshire for a further four years. In the final two winters of the study he investigated a further two grass species, namely *Arrhenatherum elatius* and *Festuca rubra* for their suitability in providing overwintering cover for polyphagous predators. Although these grasses showed promising results within the first two winters, this limited set of data warranted further investigation. If techniques for augmenting densities of beneficial predators within cereal fields are to succeed, they need to be cheap to implement and easy to maintain. For example, although *Holcus lanatus* provides good overwintering cover for predators, seed for this species is expensive and difficult to obtain. Therefore a second experiment detailed in this chapter was established to further investigate *Arrhenatherum elatius*, *Festuca rubra* and (as a standard comparison) *Dactylis glomerata*, in addition to two more grass species namely *Phleum pratense* and *Cynosurus cristatus* plus a natural regeneration treatment, as cheaper alternative overwintering cover for polyphagous predators.

2.2 MATERIALS AND METHODS

2.2.1 Comparison of polyphagous predator species composition and density within a beetle bank and two conventional hedgebanks

2.2.1.1 Study site

The study was undertaken in an 18.3ha arable field which sloped upwards from north to south (Grid ref SK 796 020) with clay soil type (Denchworth / Hanslope series), located on the Loddington Estate, Leicestershire. There were three experimental areas; the first a beetle bank measuring 400m long; the second and third consisted of 400m long hawthorn hedges, one on the western side of the field running parallel to the beetle bank (hedgebank 1) and the other on the eastern side of the field (hedgebank 2) (Fig. 1). Vegetation samples and soil cores were taken from the hedgebanks of the two hawthorn hedges. The hedge associated with hedgebank 1 divided the arable field from a pasture with a concrete yard at one end. The hedge associated with hedgebank 2 was taller and for most of its length formed the edge of a belt of a mature deciduous shelterbelt. All three areas were divided into four 100m blocks, to take into account variation in predator densities and vegetation cover along the beetle bank and hedgebanks.

2.2.1.2 Creation of the beetle bank

The bank was created on 10 September 1992 in the centre of the 18.3ha field, separating the field into two halves, of 7.48ha and 10.82ha. Two directional ploughing was used to form the bank, which measured 400m long, 2.5m wide and 0.5m high. The bank did not extend to the field margins so that a gap of 20-40 metres was left at either end to allow farm machinery to pass and the field to continue being used as a single unit. A mixture of *Dactylis glomerata* ($1.5gm^{-2}$) and *Holcus lanatus* ($2gm^{-2}$) was hand sown on the bank on 28 September 1992.

Data for the second and third winters of the beetle banks establishment were collected by previous workers in 1993 & 1994. Data for these winters were included in this study, but have been re-analysed.

Figure 1 Schematic plan of the experimental area containing the beetle bank and hedgebanks

2.2.1.3 Assessment of polyphagous predator composition

Between late November and mid December 1993, three random soil samples per block within each of the habitats were collected by taking cores to a depth of approximately 14cm, using a cylindrical borer 11.5cm in diameter (volume 1558.50 cm^3). Each soil core was sealed in a plastic bag and stored at 4^0C to inhibit predation prior to sorting (Mitchell, 1963). The cores were left for no longer than a week in cold storage. The samples were warmed by a lamp and hand sorted on a white photographic tray, and invertebrates were collected using a pooter. All invertebrates were stored in 70% methanol prior to identification. The same procedure was adopted in 1994, but hedgebank 1 was not sampled. In 1995, 1996 and 1997 the sampling programme was extended to ten random soil cores per block from the beetle bank and hedgebank 1 and five per block from hedgebank 2.

Staphylinidae and Carabidae were identified using keys from Joy (1932). In addition keys from Lindroth (1974) and Forsyth (1987) were also used in Carabidae identification. Staphylinidae were identified to genus except for *Tachyporus hypnorum* and *Tachyporus chrysomelinus* and Carabidae and Araneae to species (Araneae were identified by Mr J Daws).

The invertebrates collected were separated into three major taxonomic groups, namely Staphylinidae, Carabidae and Araneae. Where possible the Araneae were sub-divided into Linyphiidae and Lycosidae for analysis. Total Araneae, Staphylinidae and Carabidae were summed to form a fourth taxonomic group called total polyphagous predators.

Species distribution in accordance to ecological classifications were also investigated. Within the Staphylinidae *Tachyporus hypnorum* and *Tachyporus chrysomelinus* were separated from the other Staphylinidae to form a group called *Tachyporus* species. These two species have been shown by Sotherton (1984 & 1985), to overwinter in field boundaries and by Sunderland and Vickerman (1980), to prey on aphids. The total number of *Demetrias atricapillus, Agonum dorsale, Bembidion lampros, Amara plebeja, Amara familiaris* were also investigated. These carabids overwinter as adults in boundary habitats and have been found to be important predators of cereal aphids (Sotherton, 1984 &1985;

Sunderland and Vickerman, 1980). This group is termed 'highly ranked boundary carabids' in the text.

It was hypothesised that there would be a change in the carabid community structure over time within the beetle bank, from 'open-field' type carabids when the bank was first created to 'boundary' type carabids in later years. 'Open-field' type carabids are those species that are present at field centres during the winter period and are not dependant upon boundary habitats as overwintering refuges. 'Boundary' type carabids are those species that are largely dependant upon boundary habitats as overwintering refuges (Thomas, 1992b). Therefore the Carabidae were separated into the above categories for analysis.

2.2.1.4 Analysis of polyphagous predator densities

Data relating to total Carabidae, Staphylinidae and *Tachyporus* spp densities in addition to total predator densities were analysed for the years 1993, 1994, 1995, 1996 & 1997. Data for the Araneae, 'highly ranked boundary carabids' and 'boundary' type Carabidae were analysed for the years 1994, 1995, 1996 & 1997.

All data were $\log_e(x+1)$ transformed, to normalise the distributions. The data were then analysed using analysis of variance (ANOVA) within years, with block and habitat as factors, and between years within habitat, with year and block as factors, for all the above taxonomic groups. Significant differences obtained by the ANOVA were investigated using a least significant difference (LSD) multiple range test, at the 5% level.

Although individual species are mentioned in the text, differences between habitats for these individuals could not be obtained as numbers were too low for analysis.

2.2.1.5 Optimum sample size: Investigation of the relationship between sample size and the standard error of the mean of the number of polyphagous predators found in soil cores

A Pearson r test was used to investigate the relationship between sample size (ie. number of soil cores) and the standard error of the mean of the number of Carabidae, Araneae and Staphylinidae found in the soil cores. All data were $\log_e(x+1)$ transformed.

2.2.1.6 Vegetation assessment

The percentage ground cover of each soil core was estimated by eye during the winters of 1993, 1994, 1995, 1996 and 1997, for all three sites, excluding hedgebank 1 in 1994. All recordings were made in the field as the cores were being taken.

To provide a more accurate assessment of the vegetation development on the beetle bank, recordings of percentage ground cover were also taken in the summers of 1993, 1994, 1996 & 1997. Percentage cover of each species within the ground vegetation layer was recorded in a non-destructive manner, using a $0.25m^2$ quadrat. Percentage cover was estimated by eye. Ten random quadrats were taken per block. During the summers of 1996 & 1997 sampling was extended to include vegetation assessment of both the hedgebanks.

In the winter of 1993, 1995 and 1997 the structure of the vegetation within the beetle bank was assessed using a 'visimeter'. A visimeter is a metre high graduated board, marked at 5cm intervals between 0-10cm and 10cm intervals between 10-100cm. At each interval the board is sub divided into ten squares, so that when the board is viewed through the vegetation from a fixed distance the percentage of the board that is obscured at each height can be recorded. Four readings (one from each side of a $0.25m^2$ quadrat) were taken at each sampling point (ie. from where a soil core was taken) so the mean could be calculated for each height. During the winter of 1997 sampling was extended to include hedgebanks 1 & 2.

2.2.2 Assessment of overwintering habitat preference for different grass species

2.2.2.1 Study site and creation of the beetle banks

This study was performed on two 360m long beetle banks (2m wide) situated in a 8.57ha field with Hanslope and Efford (only a few plots in sections A & C) series soil type, on the Loddington Estate. These banks were created by two directional ploughing and a gap between the bank and the field margin was left to allow farm machinery to pass. Each bank was divided into two blocks of ten 18m long plots, each containing one of nine different grass treatments, sown in spring 1993. The tenth treatment was allowed to naturally regenerate. The two banks together therefore represented a randomised block design with four replicates. Five of the grass treatments contained single grass species (sowing rates in parenthesis) namely: *Dactylis glomerata* ($3gm^{-2}$), *Arrhenatherum elatius* ($6gm^{-2}$), *Festuca rubra* ($3gm^{-2}$), *Phleum pratense* ($1.8gm^{-2}$) and *Cynosurus cristatus* ($2gm^{-2}$), these plus the natural regeneration treatments were all sampled (see Appendix II for plan of beetle banks). Sowing rates were dependent upon the number of seeds per gram for each grass species.

Data for the second winter of the beetle banks establishment was collected by a previous worker in 1994. Data for this winter was included in this study, but has been re-analysed.

2.2.2.2 Assessment of polyphagous predator composition

Polyphagous predator composition was recorded as described in section 2.2.1.4. Three random soil cores per treatment were taken in the winters of 1994, 1995 & 1996. Sampling took place between January and the first two weeks in February. In 1997 the sampling programme was extended to five soil cores per treatment. To accurately assess the potential of each grass species in terms of providing a suitable habitat for overwintering predators, soil cores were taken where there was approximately 100% ground cover of the individual grass species under investigation. Thus, the data were not necessarily representative of the plots, especially where establishment of the sown species was poor. Samples from the natural regeneration treatment were taken randomly.

2.2.2.3 Analysis of polyphagous predator densities

Data relating to all taxonomic groups described in section 2.2.1.5 were analysed for the years 1994, 1995, 1996 & 1997.

All data were $\log_e(x+1)$ transformed, to normalise the distributions. The data were analysed using analysis of variance (ANOVA) with years, block and treatment (ie. the five grass treatments plus the natural regeneration treatment) as factors, for all the above taxonomic groups. Significant differences obtained by the ANOVA were investigated using an LSD multiple range test, at the 5% level.

2.2.2.4 Vegetation assessment

The percentage ground cover of each soil core taken from the natural regeneration treatments was estimated by eye, in the winters of 1994, 1995, 1996 & 1997.

In the winter of 1997 the structure of the vegetation within each grass treatment was assessed using a visimeter as described in section 2.2.1.3. Recordings were taken from each sampling point ie. from where a soil core was removed.

The establishment of the grass species within each treatment was assessed by recording percentage ground cover in the summers of 1994, 1995, 1996 & 1997. Percentage ground cover of each species was estimated by eye, using a $0.25m^2$ quadrat. Ten quadrats were taken in each grass treatment replicate plot.

2.3 RESULTS

2.3.1 Comparison of polyphagous predator species composition and density within a beetle bank and two conventional hedgebanks

2.3.1.1 Polyphagous predator composition

2.3.1.1.1 Total polyphagous predators

Total predator density comprised the total numbers of Carabidae, Staphylinidae and Araneae in 1994, 1995, 1996 and 1997. The Araneae were not recorded in 1993, therefore the data were analysed in two ways. Firstly to allow comparisons to be made with 1993 all the Araneae data was excluded from the analysis. Secondly to investigate the effect of Araneae in the total the year 1993 was excluded from any analyses. The overall results were similar (Table 1).

Total predator density remained stable within the hedgebanks throughout the study period both including and excluding Araneae. A significant year effect was recorded for the beetle bank excluding the Araneae ($F_{4,136}$ =17.76, $p<0.01$) and including the Araneae ($F_{3,125}$= 20.33, $p<0.01$).

In the second (1993) and third (1994 including & excluding Araneae) winters of the beetle bank's establishment, total predator density was significantly lower within the beetle bank compared to the hedgebanks (1993: $F_{2,30}$ = 4.40, $p<0.02$ & 1994: $F_{1,19}$ = 20.57, $p<0.01$ (incl. Araneae), $F_{1,19}$ = 24.14, $p<0.01$ (excl. Araneae)). Densities within the hedgebanks were comparable (Table. 1).

By 1995 predator density within the beetle bank was comparable to that within hedgebank 1, but significantly lower than that in hedge 2 ($F_{2,94}$ = 4.77, $p<0.01$ (incl. Araneae), $F_{2,94}$ = 20.71, $p<0.01$ (excl. Araneae)). However by the winter of 1996, predator density was greatest within the beetle bank, though only significantly greater than hedgebank 1 ($F_{2,94}$ = 13.02, $p<0.01$ (incl. Araneae), $F_{2,94}$ = 13.18, $p<0.01$ (excl. Araneae)).

Table 1. Mean total polyphagous predators (with and without Araneae) densities (m^{-2} ± one standard error) within the beetle bank, hedgebank 1 & hedgebank 2 during the winters 1993, 1994, 1995, 1996 & 1997. Hedgebank 1 was not sampled in 1994. Habitats in the same column sharing the same letters do not differ significantly within years at the 5 % level of significance (analysis of variance ($\log_e$ (x+1)) followed by an LSD multiple range test). Different italicized letters within the same column indicate significant differences within habitats between years at the 5 % level of significance (analysis of variance ($\log_e$ (x+1)) followed by an LSD multiple range test).

Site / Year	Total plus Araneae	Total minus Araneae
1993		
Beetle bank	545 ± 217.59 a/*a*	545 ± 217.59 a/*a*
Hedgebank 1	1708 ± 396.86 b/*a*	1708 ± 396.86 b/*a*
Hedgebank 2	1765 ± 565.36 b/*a*	1765 ± 565.36 b/*a*
1994		
Beetle bank	593 ± 158.87 a/*a*	457 ± 127.12 a/*a*
Hedgebank 2	3409 ± 900.26 b/*a*	3304 ± 889.66 b/*a*
1995		
Beetle bank	1246 ± 301.67 a/*b*	1157 ± 287.24 a/*b*
Hedgebank 1	1035 ± 138.87 a/*a*	958 ± 134.80 a/*a*
Hedgebank 2	1756 ± 234.91 b/*a*	1684 ± 221.41 b/*a*
1996		
Beetle bank	2180 ± 313.21 a/*c*	1973 ± 289.29 a/*c*
Hedgebank 1	885 ± 196.38 b/*a*	804 ± 191.21 b/*a*
Hedgebank 2	1896 ± 467.62 a/*a*	1752 ± 463.41 a/*a*
1997		
Beetle bank	515 ± 90.49 a/*a*	431 ± 86.08 a/*a*
Hedgebank 1	1078 ± 231.16 b/*a*	953 ± 215.24 b/*a*
Hedgebank 2	2223 ± 441.27 c/*a*	2132 ± 440.85 c/*a*

Total predator density both including and excluding the Araneae peaked in 1996 within the beetle bank, with the density in this year significantly exceeding that in all other years. Between 1996 & 1997 predator density (incl. & excl. Araneae) within the beetle bank decreased significantly to a density comparable to that in 1994. Total predator density within the beetle bank in 1997, was significantly lower than that in both hedgebanks ($F_{2,94}$ = 18.33, $p<0.01$ (incl. Araneae), $F_{2,94}$ = 20.71, $p<0.01$ (excl. Araneae)).

2.3.1.1.2 Carabidae

Twenty-one species of carabid were identified within the beetle bank, comprising 10 genera (Appendix III.i).

Total carabid density remained relatively stable within the hedgebanks throughout the study period with no significant differences between years recorded. As expected a significant year effect was recorded for the beetle bank ($F_{4,136}$ = 12.29, $p<0.00$).

Overall total carabid density within the beetle bank followed a similar pattern to that of total predator density. In the second (1993) and third (1994) winters following the beetle bank's establishment, carabid density was significantly lower within the beetle bank compared to both hedgebanks (1993: $F_{2,30}$ = 4.54, $p<0.02$ & 1994: $F_{1,19}$ = 7.24, $p<0.01$). Carabid density within the hedgebanks was comparable (Table 2).

However between 1994 and 1995 carabid density increased significantly within the beetle bank, by 133%, and in 1995 carabid density within the beetle bank was greater though not significantly so than that in hedgebank 1, and comparable to that in hedgebank 2. Between 1995 and 1996 carabid density increased again within the beetle bank, but not significantly. In 1996 carabid density within the beetle bank significantly exceeded that within hedgebank 1 and was comparable to that in hedgebank 2 ($F_{2,94}$ = 9.87, $p<0.00$). Peak densities of Carabidae were recorded in 1996 within the beetle bank and *Demetrias atricapillus* was the dominant species.

Table 2. Mean 'open-field' type carabid, 'boundary' type carabid, 'highly ranked boundary carabid' and total carabid densities (m^{-2} ± one standard error) within the beetle bank, hedgebank 1 & hedgebank 2 during the winters 1993, 1994, 1995, 1996 & 1997. Hedgebank 1 was not sampled in 1994 and the 'open-field' type carabids, 'boundary' type carabids and 'highly ranked boundary carabids' were not recorded in 1993. Habitats in the same column sharing the same letters do not differ significantly within years at the 5 % level of significance (analysis of variance ($\log_e$ (x+1)) followed by an LSD multiple range test). Different italicized letters within the same column indicate significant differences within habitats between years at the 5 % level of significance (analysis of variance ($\log_e$ (x+1)) followed by an LSD multiple range test).

Site / Year	'Open-field' species	'Boundary' species	'Highly ranked boundary carabids'	Total Carabidae
1993				
Beetle bank	-	-	-	40 ± 25.01 a/*a*
Hedgebank 1	-	-	-	369 ± 163.23 b/*a*
Hedgebank 2	-	-	-	225 ± 55.99 b/*a*
1994				
Beetle bank	40 ± 25.01	32 ± 18.10 a/*a*	0 a/*a*	80 ± 33.16 a/*a*
Hedgebank 2	16 ± 10.81	618 ± 234.40 b/*a*	56 ± 32.35 b/*a*	634 ± 236.19 b/*a*
1995				
Beetle bank	12 ± 5.10	265 ± 87.10 a/*b*	96 ± 32.69 a/*a*	301 ± 88.28 a/*b*
Hedgebank 1	5 ± 3.36	156 ± 32.27 a/*a*	55 ± 17.87 a/*a*	168 ± 34.59 a/*a*
Hedgebank 2	29 ± 17.25	207 ± 50.00 a/*a*	67 ± 29.71 a/*a*	241 ± 53.86 a/*a*
1996				
Beetle bank	60 ± 14.08	356 ± 122.14 a/*b*	642 ± 209.04 a/*b*	423 ± 121.29 a/*b*
Hedgebank 1	29 ± 7.06	75 ± 24.97 b/*a*	46 ± 16.16 b/*a*	108 ± 26.74 b/*a*
Hedgebank 2	19 ± 11.26	741 ± 375.18 a/*a*	611 ± 356.26 a/*a*	760 ± 375.17 a/*a*
1997				
Beetle bank	12 ± 5.10	63 ± 20.26 a/*a*	43 ± 17.21 a/*a*	79 ± 23.60 a/*a*
Hedgebank 1	10 ± 4.62	212 ± 96.51 a/*a*	185 ± 93.96 a/*a*	243 ± 100.53 a/*a*
Hedgebank 2	24 ± 11.84	481 ± 324.97 a/*a*	443 ± 312.06 a/*a*	515 ± 324.54 a/*a*

Carabid density fell significantly by 69% within the beetle bank between the winters of 1996 and 1997, to a level similar to that recorded in 1994. However carabid density was not significantly different from that in both hedgebanks in 1997 (Table 2).

The density of 'highly ranked boundary carabids' (ie. those carabid species that overwinter as adults in boundary habitats and which are important predators of aphids, namely *Demetrias atricapillus*, *Agonum dorsale*, *Bembidion lampros*, *Amara familiaris* and *Amara plebeja*) differed significantly between years in the beetle bank ($F_{3,125} = 17.86$, $p<0.01$) and remained relatively stable within the hedgebanks with no significant differences between years recorded. Between 1994 and 1996 the density of 'highly ranked boundary carabids' increased in the beetle bank and by 1996 the density of 'highly ranked boundary carabids' was greatest in the beetle bank but only significantly compared to hedgebank 1 ($F_{2,94} = 6.29$, $p<0.01$) (Table 2). This was due to particularly high densities of *Demetrias atricapillus* in 1996.

Analysis of the carabid community structure revealed that the density of 'boundary' type carabids differed significantly between habitats in the years 1994 ($F_{1,19} = 10.71$, $p<0.01$) and 1996 ($F_{2,94} = 10.06$, $p<0.01$). 'Boundary' type carabid density also differed significantly between years in the beetle bank ($F_{3,125} = 10.27$, $p<0.01$), though not in the hedgebanks, where 'boundary' type carabids dominated the carabid community.

In the third year (1994) following the creation of the beetle bank the densities of 'boundary' type and 'open-field' type carabids within the beetle bank were similar (Table 2). The most abundant species during this period was *Bembidion obtusum*, an 'open field' type carabid. However by 1995 'boundary' type carabid density vastly exceeded 'open-field' type carabid density on the beetle bank and 'boundary' type carabid density was comparable to that in the hedgebanks.

'Boundary' type carabid density peaked in the beetle bank during the winter of 1996 and was significantly greater than that in hedgebank 1. Although 'boundary' type carabid density fell significantly between the winters of 1996 and 1997 in the beetle bank, the density recorded in the winter of 1997 was still comparable to that found in the hedgebanks.

2.3.1.1.3 Staphylinidae

The Staphylinidae were the dominant family within the beetle bank and hedgebanks throughout the study. The most abundant staphylinids were those belonging to the Aleocharinae.

Staphylinid density remained relatively stable within the hedgebanks throughout the study period with no significant differences between years recorded. A significant year effect was recorded for the beetle bank ($F_{4,136} = 7.61$, $p<0.01$). Overall there was a general increase in staphylinid density within the beetle bank between 1993 and 1996. Staphylinid density peaked in 1996 within the beetle bank, but decreased significantly the following year to a level that was not significantly different to that in 1994 (Table 3).

Total staphylinid density was significantly greater within hedgebank 2 in 1994 compared to the beetle bank ($F_{1,19} = 25.14$, $p<0.01$) and in 1995 compared to both the beetle bank and hedgebank 1 ($F_{2,94} = 4.68$, $p<0.01$). Staphylinid density in hedgebank 1 and the beetle bank was similar. However by 1996 staphylinid density was greatest in the beetle bank but only significantly compared to hedgebank 1 ($F_{2,94} = 10.51$, $p<0.01$). As for the Carabidae, Staphylinidae density fell between 1996 and 1997, but staphylinid density in the beetle bank was still significantly greater than that in hedgebank 1 although significantly lower than that in hedgebank 2 ($F_{2,94} = 18.42$, $p<0.01$) (Table 3).

Analysis of the *Tachyporus* species (*T. hypnorum* and *T. chrysomelinus*) revealed that *Tachyporus* density differed between years within hedgebank 2 ($F_{4,76} = 4.78$, $p<0.00$) with significantly lower densities occurring in 1993 compared to 1995, 1996 and 1997 (Table 3). *Tachyporus* density remained stable in hedgebank 1. Again as expected a significant year effect was recorded within the beetle bank ($F_{4,136} = 20.86$, $p<0.00$).

In second (1993), third (1994) and fourth (1995) winters of the beetle bank's establishment, *Tachyporus* density was not significantly different from that within both hedgebanks. Between the winters of 1995 & 1996, *Tachyporus* density increased significantly by 143% within the beetle bank, and in 1996 *Tachyporus* density was significantly greater within the beetle bank ($F_{2,94} = 22.59$, $p<0.00$) compared to both

Table 3. Mean *Tachyporus* species and total staphylinid densities (m^{-2} ± one standard error) within the beetle bank, hedgebank 1 & hedgebank 2 during the winters 1993, 1994, 1995, 1996 & 1997. Hedgebank 1 was not sampled in 1994. Habitats in the same column sharing the same letters do not differ significantly within years at the 5 % level of significance (analysis of variance ($\log_e$ (x+1)) followed by an LSD multiple range test). Different italicized letters in the same column indicate significant differences within habitats between years at the 5 % level of significance (analysis of variance ($\log_e$ (x+1)) followed by an LSD multiple range test).

Site / Year	*Tachyporus* species	Total Staphylinidae
1993		
Beetle bank	56 ± 32.35 a/*a*	505 ± 204.90 a/*a*
Hedgebank 1	96 ± 33.51 a/*a*	1339 ± 342.23 a/*a*
Hedgebank 2	72 ± 31.26 a/*a*	1540 ± 543.29 a/*a*
1994		
Beetle bank	64 ± 27.36 a/*ab*	377 ± 105.60 a/*ab*
Hedgebank 2	465 ± 326.57 a/*ab*	2671 ± 679.24 b/*a*
1995		
Beetle bank	354 ± 163.12 ab/*b*	857 ± 205.70 a/*b*
Hedgebank 1	99 ± 22.73 a/*a*	789 ± 122.14 a/*a*
Hedgebank 2	390 ± 98.86 b/*b*	1444 ± 208.31 b/*a*
1996		
Beetle bank	1044 ± 200.93 a/*c*	1550 ± 239.10 a/*c*
Hedgebank 1	183 ± 34.77 b/*a*	695 ± 169.23 b/*a*
Hedgebank 2	428 ± 119.62 c/*b*	991 ± 158.78 a/*a*
1997		
Beetle bank	214 ± 56.15 a/*ab*	351 ± 74.75 a/*a*
Hedgebank 1	219 ± 51.35 a/*a*	710 ± 142.87 b/*a*
Hedgebank 2	568 ± 135.74 b/*b*	1622 ± 347.95 c/*a*

hedgebanks. *Tachyporus* density reached its peak in 1996, within the beetle bank, with the density in 1996 significantly exceeding that in any other year.

Tachyporus density decreased significantly by 62% between 1996 & 1997. However although *Tachyporus* density was significantly greater within hedgebank 2 compared to both hedgebank 1 and the beetle bank in 1997 ($F_{2,94} = 8.42$, $p<0.00$), *Tachyporus* density within the beetle bank was still comparable to that within hedgebank 1. *Tachyporus* density within the beetle bank in 1997, was also comparable to that in years prior to 1996 (Table 3).

The dominant *Tachyporus* species was *Tachyporus hypnorum*.

2.3.1.1.4 Araneae

Araneae density remained relatively stable in both hedgebanks, with no significant differences recorded between years. However a significant year effect was recorded within the beetle bank ($F_{3,125} = 4.40$, $p<0.01$). Araneae density fluctuated between years in the beetle bank, with the peak density recorded in 1996 only being significantly greater than that in 1995 and 1997 (Table 4). Araneae density was generally greatest within the beetle bank, throughout the study, but only significantly so in 1996 ($F_{2,94} = 6.55$, $p<0.00$), compared to hedgebank 1.

Only changes in linyphiid density could be analysed as the number of Lycosidae and other species, caught were too low for statistical analysis. Any trends interpreted from the lycosid and other species data should therefore be viewed with caution. Linyphiid density remained relatively stable within the beetle bank and hedgebanks throughout the study, and densities of linyphiids in the beetle bank and hedgebanks were similar. Lycosid density on the other hand fluctuated greatly between years in the beetle bank, with particularly high densities recorded in the winter of 1996 (Table 4). Overall lycosid density appeared to be greater in the beetle bank compared to the hedgebanks, where the linyphiids dominated the Araneae. With the exception of the winter of 1996, linyphiid and lycosid densities were similar on the beetle bank overtime. Other species of Araneae were less abundant compared to the Linyphiidae and Lycosidae, in both the beetle bank and

Table 4. Mean Linyphiidae, Lycosidae, other Araneae species and total Araneae densities (m^{-2} ± one standard error) within the beetle bank, hedgebank 1 & hedgebank 2 during the winters 1994, 1995, 1996 & 1997. Hedgebank 1 was not sampled in 1994 and Araneae were not recorded in 1993. Habitats in the same column sharing the same letters do not differ significantly within years at the 5 % level of significance (analysis of variance ($\log_e$ (x+1)) followed by an LSD multiple range test). Different italicized letters within the same column indicate significant differences within habitats between years at the 5 % level of significance (analysis of variance ($\log_e$ (x+1)) followed by an LSD multiple range test).

Site / Year	Linyphiidae	Lycosidae	Other Araneae	Total Araneae
1993				
Beetle bank	-	-	-	-
Hedgebank 1	-	-	-	-
Hedgebank 2	-	-	-	-
1994				
Beetle bank	72 ± 29.32 a/*a*	72 ± 29.32	0	136 ± 52.26 a/*ab*
Hedgebank 2	96 ± 31.34 a/*a*	24 ± 12.57	0	104 ± 27.68 a/*a*
1995				
Beetle bank	31 ± 9.37 a/*a*	25 ± 7.23	6 ± 3.46	89 ± 20.50 a/*a*
Hedgebank 1	72 ± 36.59 a/*a*	0	5 ± 3.36	77 ± 36.50 a/*a*
Hedgebank 2	43 ± 20.33 a/*a*	0	29 ± 14.14	72 ± 28.68 a/*a*
1996				
Beetle bank	41 ± 12.37 a/*a*	144 ± 25.79	22 ± 10.61	207 ± 36.40 a/*ab*
Hedgebank 1	60 ± 20.00 a/*a*	19 ± 8.58	2 ± 2.00	77 ± 36.50 b/*a*
Hedgebank 2	115 ± 33.92 a/*a*	14 ± 10.53	19 ± 8.83	72 ± 28.68 ab/*a*
1997				
Beetle bank	51 ± 12.42 a/*a*	26 ± 9.74	12 ± 5.10	84 ± 16.23 a/*a*
Hedgebank 1	111 ± 25.92 a/*a*	10 ± 4.62	7 ± 4.06	125 ± 26.52 a/*a*
Hedgebank 2	82 ± 24.46 a/*a*	0	10 ± 6.62	91 ± 26.57 a/*a*

hedgebanks throughout the study period (Table 4). Changes in the Araneae species composition of the beetle bank are shown in Appendix III. ii.

2.3.1.2 Optimum sample size: Investigation of the relationship between sample size and the standard error of the mean of the number of polyphagous predators found in soil cores

Large standard errors were obtained throughout the study. Therefore the relationship between sample size and the standard error of the mean of the number of Carabidae, Araneae and Staphylinidae found in soil cores was investigated, to estimate how many soil cores would have to be taken to reduce the standard error to an acceptable level.

A negative relationship was found between sample size and the standard error of the mean of the number of Carabidae, Araneae and Staphylinidae found in the soil cores (Table 5). Although the standard error was reduced by approximately half by increasing the sample size from 12 to 40, it was estimated that an optimum sample size of approximately 120 cores per site would have to be taken to reduce the standard error to an acceptable level.

Table 5. Results of correlations between sample size and the standard error of polyphagous predators found in soil cores (all data $\log_e (x+1)$ transformed) (* $p<0.05$)

Predatory group	r value, significance of correlation
Carabidae	r = -0.70*
Staphylinidae	r = -0.82*
Araneae	r = -0.85*

2.3.1.3 Vegetation assessment

By the summer of 1993, *Dactylis glomerata* and *Holcus lanatus* had become firmly established on the beetle bank, with percentage ground cover over the bank similar at 38 % and 35 % respectively (Fig. 2). Less than 5% of the bank was bare. Other species present on the bank in this year were *Polygonum aviculare*, *Polygonum persicaria*, *Avena fatua* and *Elytrigia repens* (Appendix IV.i). By 1994, *Dactylis glomerata* was out competing *Holcus lanatus* which averaged approximately 18% of the bank's ground cover compared to approximately 65% for *Dactylis glomerata* (Fig. 2). It was noted that *Holcus lanatus* was only present at the edges of the beetle bank whilst *Dactylis glomerata* dominated the rest of the bank. This trend continued with *Dactylis glomerata* dominating the bank at the expense of *Holcus lanatus* in 1996 & 1997 (Fig. 2).

Elytrigia repens was the dominant species in hedgebanks 1 (1996 23% & 1997 32%) and 2 (1996 75% & 1997 67% respectively). A wide range of other species were also present but in smaller numbers within both hedgebanks. Overall the flora was more diverse in the hedgebanks compared to the beetle bank (Appendix IV.ii & IV. iii).

Dactylis glomerata dominated the ground cover of the soil cores taken from the beetle bank between 1993 and 1997 (Appendix IV. iv). *Elytrigia repens* dominated the ground cover of the soil cores in both hedgebanks in 1993, and hedgebank 2 in 1994 (Appendix IV. v & IV. vi). Litter dominated the soil cores from both the hedgebanks in 1995, and hedgebank 1 in 1996. *Elytrigia repens* also dominated the soil cores in 1996 & 1997 within hedgebanks 1 & 2.

Vegetation height increased within the beetle bank between the winters of 1993 and 1997 (Fig. 3). Overall the vegetation within the beetle bank was higher (up to 90-100m) than that in the hedgebanks (up to approximately 80-90cm in hedgebank 1 & 30-40cm in hedgebank 2). The vegetation near to ground level was also denser within the beetle bank compared to the hedgebanks. Means for the visimeter recordings from the beetle bank and hedgebanks are given in Appendix IV.vii & IV.viii.

Fig. 2. Mean percentage ground cover of the vegetation on the beetle bank in the summers of 1993, 1994, 1996 & 1997

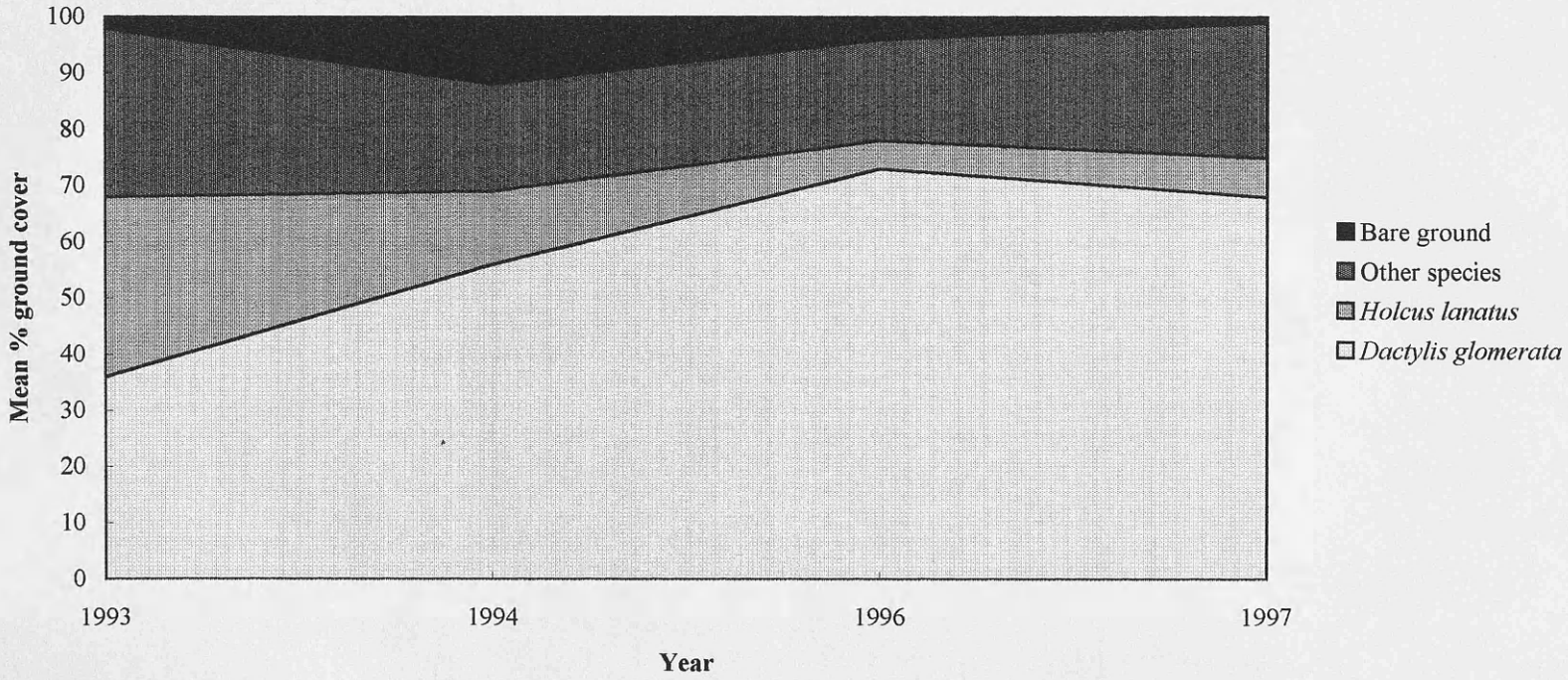
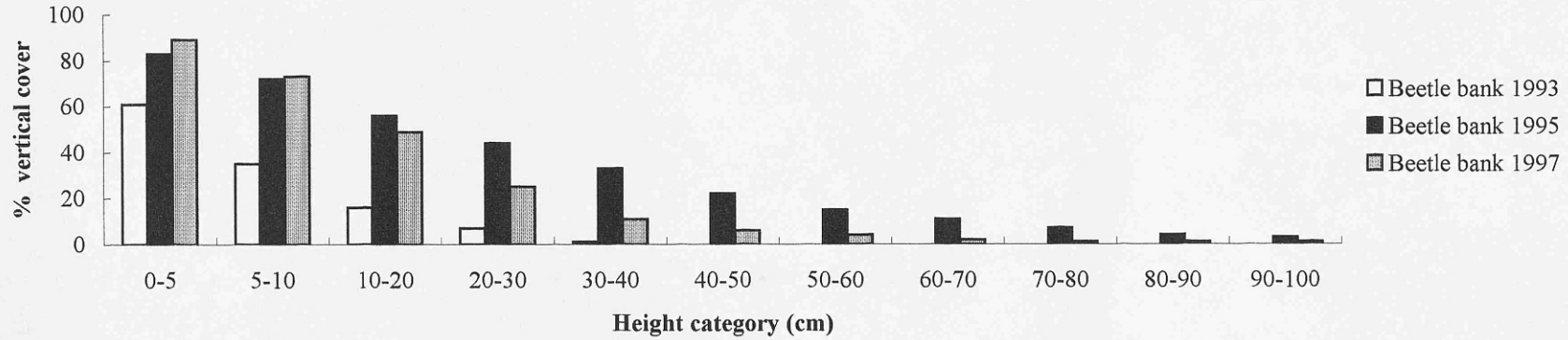
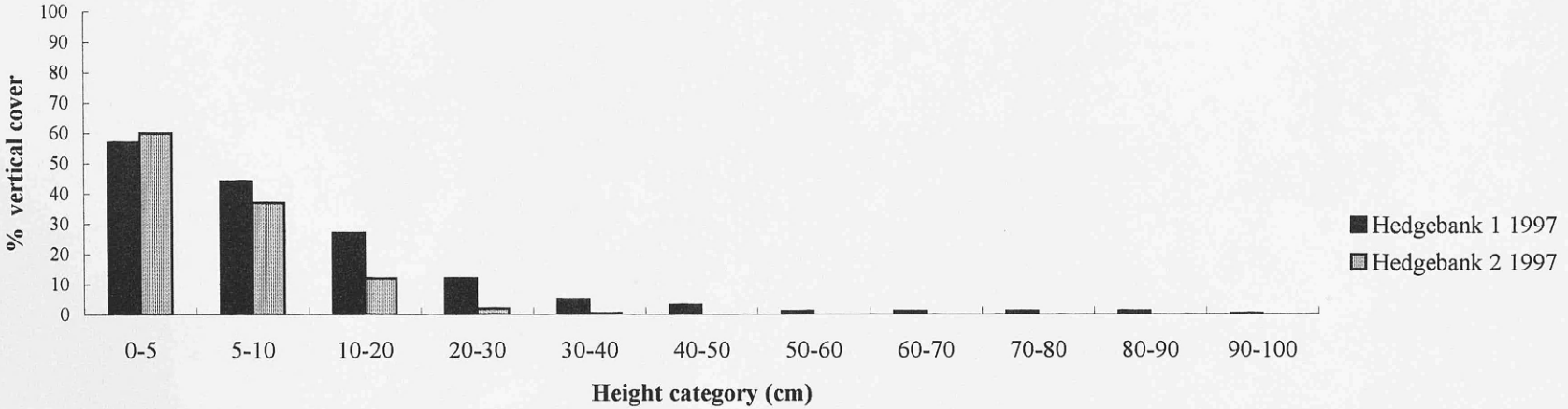


Fig. 3. Mean percentage vertical cover of the vegetation on the beetle bank in the winters of 1993, 1995 & 1997, and on the hedgebanks in the winter of 1997





2.3.2 Assessment of overwintering habitat preference for different grass species

2.3.2.1 Polyphagous predator composition

2.3.2.1.1 Total polyphagous predators

Total polyphagous predator density comprised total Carabidae, total Staphylinidae and total Araneae.

Total predator density differed significantly between treatments ($F_{5,309} = 3.61$, $p<0.01$) and between years ($F_{3,309} = 16.97$, $p<0.01$) . Overall total predator density was greatest in *A. elatius* but only significantly compared to *C. cristatus*, *F. rubra* and the natural regeneration treatment (Table 6). Total predator density was also significantly greater within *D. glomerata* and *P. pratense* compared to the natural regeneration treatment.

Overall there was a significant increase in predator density within the treatments from 1994 to 1996. Total predator density peaked in 1996 and was significantly greater than that in any other year. Although predator density fell significantly between the years 1996 & 1997, total predator density was not significantly different to that immediately prior to the peak in 1995 (Table 6).

Table 6. Mean total polyphagous predator densities (m^{-2} ± one standard error) within the five single grass treatments and the natural regeneration treatment between the winters 1994 & 1997. Significant differences between treatments are shown in the final row. Treatments in the same row sharing the same letter do not differ significantly at the 5 % level of significance (analysis of variance ($\log_e(x+1)$) followed by an LSD multiple range test). Significant differences between years are shown in the final column. Years sharing the letter do not differ significantly at the 5 % level of significance (analysis of variance ($\log_e(x+1)$) followed by an LSD multiple range test).

Year	Natural regeneration	*Phleum pratense*	*Arrhenatherum elatius*	*Cynosurus cristatus*	*Dactylis glomerata*	*Festuca rubra*	Mean total for each year
1994	626 ± 265.57	842 ± 164.64	1756 ± 907.76	449 ± 97.93	1500 ± 344.07	642 ± 185.56	969 ± 176.95 a
1995	1283 ± 323.00	1933 ± 558.88	1564 ± 354.25	866 ± 147.02	1436 ± 249.20	1075 ± 323.54	1359 ± 143.26 b
1996	1323 ± 220.41	3040 ± 809.21	2823 ± 685.12	2478 ± 442.66	2382 ± 612.98	2150 ± 587.40	2366 ± 241.25 c
1997	1030 ± 259.49	953 ± 204.75	2040 ± 552.08	1588 ± 300.69	1328 ± 247.12	1858 ± 428.39	1466 ± 145.92 b
Mean total for each treatment	1060 ± 138.16 a	1586 ± 247.48 bcd	2045 ± 319.38 d	1380 ± 174.00 ac	1614 ± 185.41 cd	1492 ± 222.35 ab	-

2.3.2.1.2 Carabidae

Twenty-seven species of Carabidae were identified from the two banks over the four year study period (Appendix V.i). Six species were common throughout the study period on the banks namely *Amara plebeja, Bembidion lampros, Bembidion obtusum, Bembidion guttula, Demetrias atricapillus* and *Trechus quadristriatus.*

Total carabid density was significantly greater in *D. glomerata* compared to all the other treatments ($F_{5,309} = 2.99$, $p<0.01$) (Table 7).

D. glomerata also supported a significantly greater density of 'highly ranked boundary carabids' compared to any other treatment ($F_{5,309} = 4.96$, $p<0.01$) (Table 7). 'Highly ranked boundary carabid' density was lowest in *C. cristatus* and the natural regeneration treatment. Several of the carabid species belonging to this group were common to each of the treatments throughout the study period. *Demetrias atricapillus* was common to *D. glomerata, F. rubra* and *A. elatius, Bembidion lampros* was common to *D. glomerata* and *F. rubra* and *Amara plebeja* was common to *P. pratense, F. rubra* and *A. elatius.* None of the Carabidae were common to *C. cristatus* or the natural regeneration treatment. A significant year effect was also recorded for the 'highly ranked boundary carabids' ($F_{3,309} = 4.02$, $p<0.01$) with significantly lower densities recorded in 1994 compared to any other year (Table 7).

Analysis of the carabid community structure revealed a significant difference between the density of 'boundary' type carabids in the six treatments ($F_{5,309} = 5.50$, $p<0.01$). As for the other carabid groups, 'boundary' type carabid density was significantly greater in *Dactylis glomerata* compared to any other treatment. Overall 'boundary' type carabid dominated the treatments, whilst 'open-field' type carabids were present in lower numbers (Table 7).

Table 7. Mean total Carabidae, 'highly ranked boundary carabid', 'boundary' and 'open-field' type Carabidae densities (m^{-2} ± one standard error) within the five single grass treatments and the natural regeneration treatment between the winters 1994 & 1997. Significant differences between treatments are shown in the final row for each taxonomic group. Treatments in the same row sharing the same letter do not differ significantly at the 5 % level of significance (analysis of variance ($\log_e$ (x+1)) followed by an LSD multiple range test). Significant differences between years for each taxonomic group are shown in the final column. Years sharing the letter do not differ significantly at the 5 % level of significance (analysis of variance ($\log_e$ (x+1)) followed by an LSD multiple range test).

Year	Natural regeneration	*Phleum pratense*	*Arrhenatherum elatius*	*Cynosurus cristatus*	*Dactylis glomerata*	*Festuca rubra*	Mean total for each year
Total Carabidae							
1994	24 ± 17.27	160 ±87.33	80 ± 23.20	48 ± 22.16	449 ± 173.44	104 ± 38.31	144 ± 36.52 a
1995	249 ± 53.59	152 ± 49.50	257 ± 108.15	128 ± 32.08	144 ± 48.12	104 ± 34.46	172 ± 24.60 b
1996	56 ± 18.58	88 ± 22.03	136 ± 38.31	48 ± 25.13	569 ± 357.47	120 ± 26.82	170 ± 62.11 ab
1997	144 ± 56.51	135 ± 47.50	125 ± 44.22	159 ± 72.99	298 ± 135.02	173 ± 41.07	172 ± 29.94 ab
Mean total for each treatment	122 ± 25.78 a	134 ± 27.16 a	146 ± 29.94 a	105 ± 28.21 a	356 ± 97.58 b	132 ± 19.24 a	-
'Highly ranked boundary carabids'							
1994	0	48 ± 40.18	24 ± 12.57	0	168 ± 144.19	24 ± 12.57	44 ± 25.18 a
1995	56 ± 27.68	64 ± 34.20	176 ± 104.52	24 ± 17.27	80 ± 23.20	56 ± 18.58	76 ± 19.87 b
1996	16 ± 10.81	56 ± 18.58	56 ± 25.01	24 ± 12.57	529 ± 343.87	96 ± 23.69	130 ± 59.66 b
1997	58 ± 39.13	43 ± 14.77	67 ± 21.06	120 ± 68.37	265 ± 127.20	87 ± 26.03	107 ± 26.04 b
Mean total for each treatment	36 ± 15.43 a	52 ± 12.74 ab	79 ± 24.66 ab	53 ± 25.36 a	261 ± 91.76 c	69 ± 11.94 b	-
'Boundary' Carabidae							
1994	8 ± 8.00	144 ± 84.19	56 ± 14.31	24 ± 17.27	393 ± 173.90	56 ± 22.03	114 ± 35.17 a
1995	88 ± 43.46	96 ± 44.33	233 ± 102.91	56 ± 27.68	112 ± 33.16	64 ± 21.63	108 ± 21.95 a
1996	24 ± 12.57	64 ± 18.10	112 ± 33.16	24 ± 12.57	561 ± 358.13	120 ± 26.82	151 ± 62.21 a
1997	130 ± 53.30	82 ± 26.38	111 ± 40.88	130 ± 68.15	279 ± 132.83	96 ± 28.79	138 ± 28.10 a
Mean total for each treatment	72 ± 22.11 a	95 ± 22.41 ac	125 ± 27.96 c	69 ± 25.81 a	328 ± 97.17 b	86 ± 13.58 ac	-
'Open-field' Carabidae							
1994	8 ± 8.00	8 ± 8.00	8 ± 8.00	24 ± 17.27	40 ± 18.58	48 ± 22.16	23 ± 6.17
1995	88 ± 40.10	32 ± 13.68	16 ± 10.81	64 ± 21.63	32 ± 4.66	40 ± 18.58	45 ± 9.70
1996	24 ± 17.27	16 ± 10.81	24 ± 12.57	16 ± 16.00	8 ± 8.00	8 ± 8.00	16 ± 5.04
1997	5 ± 5.00	38 ± 24.59	10 ± 10.00	29 ± 12.29	5 ± 5.00	77 ± 29.29	27 ± 7.22
Mean total for each treatment	27 ± 10.32	26 ± 9.65	14 ± 5.16	33 ± 8.24	19 ± 7.12	48 ± 12.51	-

2.3.2.1.3 Staphylinidae

The Staphylinidae were the dominant family in all the treatments throughout the study and the most abundant species was *Tachyporus hypnorum*.

Total staphylinid density differed significantly between treatments ($F_{5,309} = 2.64$, $p<0.02$). *A. elatius* supported the highest density of staphylinids but only significantly compared to the natural regeneration treatment, *F. rubra* and *C. cristatus* (Table 8). A significant year effect ($F_{3,309} = 21.01$, $p<0.01$) was also recorded for the Staphylinidae. Staphylinid density was significantly lower in 1994 and higher in 1996 compared to any other year.

Analysis of the *Tachyporus* species revealed a significant interaction between year and species ($F_{15,309} = 2.07$, $p<0.01$) (Table 8). In the first year of the study *Tachyporus* density was greatest within *A. elatius*, but only significantly compared to *C. cristatus*, *F. rubra* and the natural regeneration treatment (Table 8). *Tachyporus* density generally increased within all of the treatments from 1994 to 1996. *Tachyporus* density was greatest in *D. glomerata* in 1995 but only significantly compared to *C. cristatus*.

Between 1995 and 1996 *Tachyporus* density increased by 156% within *A. elatius*, and in 1996 this grass supported the highest density of *Tachyporus* species. However *Tachyporus* density was only significantly higher within *A. elatius* compared to the natural regeneration treatment, where *Tachyporus* density was lowest. Surprisingly *Tachyporus* density was third highest in *C. cristatus*. This grass supported the lowest densities of *Tachyporus* in the first two years of the study, but between 1995 and 1996 *Tachyporus* density increased significantly by 184%.

Peak *Tachyporus* density was recorded within all the treatments in 1996, but only the densities in *C. cristatus*, *P. pratense* and *A. elatius* were significantly different to those in any other year within the respective species. *Tachyporus* density fell in 1997 within all the treatments, but densities were not significantly different to those before the peak, with the exception of *P. pratense* where *Tachyporus* density fell to a level similar to that in 1994. In 1997 *Tachyporus* density was greatest in *F. rubra* but only significantly compared to *P. pratense*, the natural regeneration treatment and *D. glomerata* (Table 8).

Table 8. Mean total Staphylinidae and *Tachyporus* species densities (m^{-2} ± one standard error) within the five single grass treatments and the natural regeneration treatment between the winters 1994 & 1997. Significant differences between treatments are shown in the final row for each taxonomic group. Treatments in the same row sharing the same letter do not differ significantly at the 5 % level of significance (analysis of variance ($\log_e(x+1)$) followed by an LSD multiple range test). Significant differences between years for each taxonomic group are shown in the final column. Years sharing the letter do not differ significantly at the 5 % level of significance (analysis of variance ($\log_e(x+1)$) followed by an LSD multiple range test). (*Tachyporus* species showed a significant interaction between year and treatment (analysis of variance ($\log_e(x+1)$). Treatments in the same year sharing the same letters do not differ significantly at the 5% level of significance (analysis of variance ($\log_e(x+1)$) followed by an LSD multiple range test). Different italicized letters within the same column indicate significant differences within treatments between years at the 5% level of significance (analysis of variance ($\log_e(x+1)$) followed by an LSD multiple range test)).

Taxonomic group / Year	Natural regeneration	*Phleum pratense*	*Arrhenatherum elatius*	*Cynosurus cristatus*	*Dactylis glomerata*	*Festuca rubra*	Mean total for each year
Total Staphylinidae							
1994	497 ± 220.95	521 ± 118.15	1436 ± 800.49	249 ± 78.99	874 ± 247.79	393 ± 138.39	662 ± 150.33 a
1995	946 ± 258.70	1700 ± 469.02	1203 ± 288.13	658 ± 120.72	113 ± 220.73	903 ± 306.96	1095 ± 122.78 b
1996	1147 ± 208.41	2607 ± 742.07	2494 ± 626.49	2133 ± 391.64	1508 ± 439.04	1845 ± 519.63	1956 ± 212.53 c
1997	780 ± 192.86	712 ± 166.62	1723 ± 513.95	1270 ± 268.58	905 ± 179.98	1574 ± 426.06	1161 ± 132.83 b
Mean total for each treatment	834 ± 110.92 a	1289 ± 221.20 bc	1715 ±290.04 b	1105 ± 155.89 ac	1076 ± 134.40 bc	1241 ± 210.10 ac	-
Tachyporus species							
1994	321 ± 165.58 a/*a*	305 ± 107.82 ab/*ac*	858 ± 378.82 b/*a*	136 ± 73.47 a/*a*	377 ± 124.51 ab/*a*	168 ± 83.04 a/*a*	361 ± 78.92
1995	513 ± 166.42 ab/*ab*	770 ± 247.66 a/*a*	265 ± 82.19 ab/*a*	225 ± 77.08 b/*ac*	577 ± 158.50 a/*ab*	602 ± 295.50 ab/*ac*	492 ± 77.76
1996	754 ± 179.61 a/*b*	1981 ± 533.31 b/*b*	1925 ± 557.82 b/*b*	1339 ± 212.08 ab/*b*	938 ± 212.63 ab/*b*	1436 ± 474.54 ab/*bc*	1396 ± 165.19
1997	457 ± 148.26 ac/*ab*	241 ± 77.91 a/*c*	751 ± 201.36 abc/*a*	703 ± 206.44 abc/*c*	332 ± 79.14 ac/*a*	1020 ± 283.32 bc/*c*	584 ± 76.58
Mean total for each treatment	504 ± 82.74	741 ± 156.29	921 ± 174.89	615 ± 106.08	524 ± 73.86	837 ± 164.82	-

Overall those species that supported the highest *Tachyporus* density in the first two years of the study, supported the lowest densities in the final year of the study and visa versa, with the exception of *A. elatius*.

2.3.2.1.4 Araneae

Total Araneae density differed between treatments ($F_{5,309} = 2.34$, $p<0.04$) and between years ($F_{3,309} = 4.94$, $p<0.01$). The highest overall density was recorded in *D. glomerata*, but this was only significant compared to *F. rubra* and the natural regeneration treatment (where Araneae density was lowest) (Table 9). Total Araneae density fluctuated between years, peaking in 1996 though only significantly compared to 1995 & 1997.

The Lycosidae and Linyphiidae were the most abundant families during the study. No significant differences were recorded for either of these families between treatments, although both liniphiid and lycosid density did differ significantly between years ($F_{3,309} = 14.64$, $p<0.01$; $F_{3,309} = 11.83$, $p<0.01$ respectively). Overall linyphiid density was greatest in 1994 and lycosid density was greatest in 1996 (Table 9).

Changes in the Araneae species composition on the beetle banks overtime are shown in Appendix V. ii.

Table 9. Mean total Araneae, Linyphiidae, Lycosidae and other Araneae densities (m^{-2} ± one standard error) within the five single grass treatments and the natural regeneration treatment between the winters 1994 & 1997. Significant differences between treatments are shown in the final row for each taxonomic group. Treatments in the same row sharing the same letter do not differ significantly at the 5 % level of significance (analysis of variance ($\log_e (x+1)$) followed by an LSD multiple range test). Significant differences between years for each taxonomic group are shown in the final column. Years sharing the letter do not differ significantly at the 5 % level of significance (analysis of variance ($\log_e (x+1)$) followed by an LSD multiple range test).

Year	Natural regeneration	*Phleum pratense*	*Arrhenatherum elatius*	*Cynosurus cristatus*	*Dactylis glomerata*	*Festuca rubra*	Mean total for each year
Total Araneae							
1994	104 ± 56.14	160 ± 54.72	241 ± 95.88	152 ± 45.05	176 ± 38.99	144 ± 43.53	163 ± 23.67 ac
1995	96 ± 33.51	136 ± 43.46	104 ± 32.35	80 ± 28.61	160 ± 71.41	40 ± 18.58	103 ± 16.69 b
1996	120 ± 51.81	345 ± 100.85	192 ± 73.99	297 ± 66.45	281 ± 81.61	184 ± 64.30	237 ± 30.81 c
1997	106 ± 25.08	106 ± 27.84	192 ± 44.71	149 ± 30.81	125 ± 29.71	111 ± 35.10	132 ± 13.43 ab
Mean total for each	107 ± 19.42 a	175 ± 29.85 bc	184 ± 30.95 bc	167 ± 22.94 bc	177 ± 2.18 b	119 ± 21.66 ac	-
Linyphiidae							
1994	104 ± 56.14	128 ± 43.26	152 ± 69.54	152 ± 45.05	136 ± 32.35	112 ± 30.97	131 ± 19.07 a
1995	24 ± 12.57	40 ± 25.01	40 ± 14.31	0	64 ± 34.20	16 ± 10.81	31 ± 8.04 b
1996	56 ± 27.68	120 ± 49.03	72 ± 31.62	96 ± 41.04	96 ± 63.80	48 ± 22.16	82 ± 16.67 c
1997	24 ± 9.56	34 ± 14.44	48 ± 13.06	63 ± 21.26	19 ± 8.83	29 ± 15.77	36 ± 5.93 b
Mean total for each	48 ± 14.30 a	74 ± 16.45 a	74 ± 17.68 a	76 ± 16.21 a	70 ± 17.77 a	48 ± 10.97 a	-
Lycosidae							
1994	0	16 ± 10.81	64 ± 29.81	0	32 ± 18.10	8 ± 8.00	20 ± 6.58 a
1995	48 ± 18.73	80 ± 23.20	56 ± 27.68	80 ± 28.61	88 ± 43.46	24 ± 17.27	63 ± 11.29 b
1996	56 ± 32.35	209 ± 73.83	112 ± 63.62	160 ± 29.81	128 ± 34.20	96 ± 41.04	127 ± 20.04 c
1997	67 ± 18.61	63 ± 28.17	120 ± 45.72	72 ± 20.80	67 ± 19.87	91 ± 28.34	80 ± 11.52 b
Mean total for each	46 ± 10.69 a	88 ± 20.99 a	93 ± 22.74 a	77 ± 13.30 a	77 ± 14.60 a	60 ± 14.63 a	-
Other Araneae							
1994	0	16 ± 16.00	24 ± 12.57	0	8 ± 8.00	8 ± 8.00	9 ± 3.88
1995	24 ± 24.00	16 ± 10.81	8 ± 8.00	0	8 ± 6.00	0	9 ± 4.72
1996	8 ± 8.00	16 ± 10.81	8 ± 8.00	32 ± 13.68	56 ± 40.10	40 ± 18.58	27 ± 8.13
1997	14 ± 7.88	10 ± 6.62	29 ± 14.14	14 ± 14.00	43 ± 19.09	0	18 ± 5.00
Mean total for each	12 ± 6.04	14 ± 5.16	19 ± 6.21	12 ± 6.04	31 ± 11.27	10 ± 4.70	-

2.3.2.2 Vegetation assessment

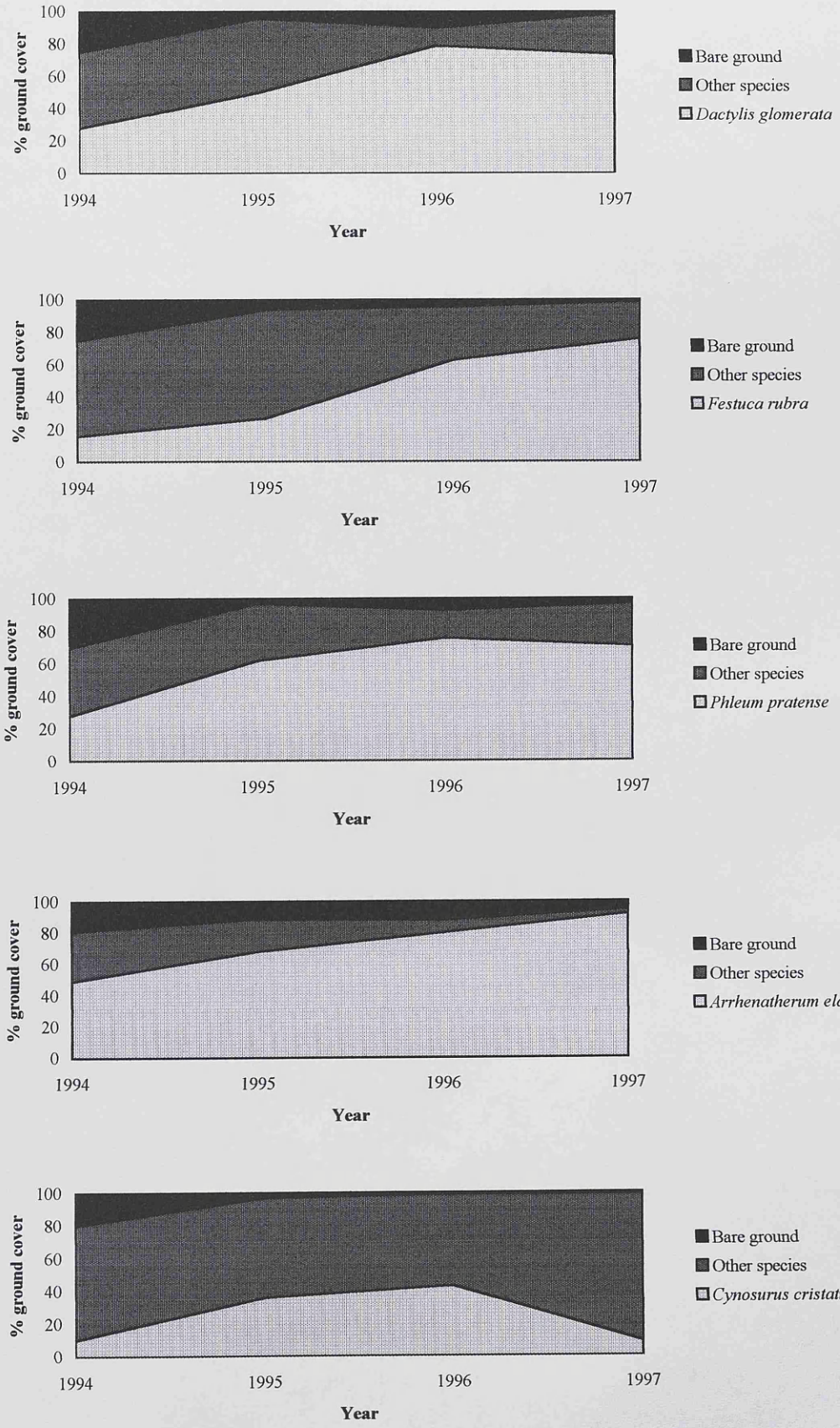
By 1995 all the single sown grass species dominated their allotted plots (Fig. 4), although the *F. rubra* plots (27% of the ground cover comprised *F. rubra*) also contained a high percentage of *Lolium perenne* (23%) and *Poa trivialis* (16%). The *C. cristatus* plots (36% of the ground cover comprised *C. cristatus*) also contained a high percentage of *Poa trivialis* (24%). In the final year of the study *A. elatius* (90%) provided the greatest cover in its allotted plots compared to *F. rubra* (75%), *D. glomerata* and *P. pratense* (70%) and *C. cristatus* (10%). The *C. cristatus* plots were dominated by *Elytrigia repens* (31%) in the final year of the study along with a multitude of other species in smaller numbers (Appendix VI. i). The natural regeneration treatments were mainly dominated by *Elytrigia repens* and *Ranunculus repens* and *Festuca rubra* in the final year (Appendix VI. ii).

The results from the visimeter indicated that *D. glomerata*, *A. elatius* and *P. pratense* all formed dense grass swards and grew to at least 70-80cm tall. *F. rubra* and *C. cristatus* were much shorter species growing up to 40-50cm tall (Appendix VI. vii). The visimeter recordings portrayed a reasonably accurate estimate of the height of the vegetation in the above treatments, as personal observations indicated that vegetation height was almost uniform in these plots. However although vegetation was found growing to 80-90 cm in the natural regeneration plots (Appendix VI. vii), many of the plots were covered by low growing species such as *Ranunculus repens*.

The ground cover of the soil cores taken from the natural regeneration treatments were dominated by *Poa trivialis* in 1994 (plus a large percentage of bare ground) and 1995, whilst *Elytrigia repens* and *Festuca rubra* dominated in 1996 and 1997 respectively (Appendix VI. viii).

The raw data for all the vegetation samples are presented in Appendix VI.

Fig. 4. Mean percentage ground cover of the vegetation in the *Dactylis glomerata*, *Festuca rubra*, *Phleum pratense*, *Arrhenatherum elatius* and *Cynosurus cristatus* plots in the summers 1994, 1995, 1996 and 1997.



2.4 DISCUSSION

2.4.1 Comparison of polyphagous predator species composition and density within a beetle bank and two conventional hedgebanks

Pioneering work by Thomas *et al.* (1991 & 1992b) and MacLeod (1994), showed that beetle banks located in Hampshire supported high densities of overwintering polyphagous predators, with densities sustained at levels comparable to or greater than those found in surrounding field boundaries over a seven year period.

The present study has shown that these results can be replicated elsewhere in the UK, under different conditions such as soil type. The beetle bank in Leicestershire provided a suitable overwintering habitat for the Staphylinidae and the Araneae by the second and third winters respectively of the beetle banks establishment, with densities comparable to those in surrounding field margins. Carabid density in the beetle bank was comparable to that in the field margins by the fourth winter. Polyphagous predator densities were not recorded after the first winter of the beetle bank's creation, as the grasses sown on the bank had not established.

Polyphagous predator densities fluctuated over the five year study period within the beetle bank. The general trend indicated an increase in predator densities on the beetle bank up until the fifth winter, when peak densities of all taxonomic groups were recorded. The densities of 'highly ranked boundary carabids', Araneae and *Tachyporus* spp fell in the sixth winter to levels comparable to those immediately before the peak, whereas the densities of the Carabidae, 'boundary' type Carabidae and Staphylinidae fell in the sixth winter to a level similar to that in the third winter. Similar fluctuations in predator population density were recorded over a seven year period on beetle banks in Hampshire (MacLeod, 1994). Between-year fluctuations in predator density within the beetle bank may have been influenced by a number of different factors throughout the year, for example: meteorological conditions during the summer. The summer of 1996 was warm and dry providing excellent conditions for cereal aphids. The abundance of cereal aphids and possibly other prey may have enhanced the summer survival of both adult and larval polyphagous predators, which would have increased overwintering populations in the

beetle bank that winter. However polyphagous predator populations remained stable within the hedgebanks during the study, indicating that other factors were also affecting the changes in polyphagous predator density within the beetle bank. These are discussed below.

The length of time over which it took the Carabidae, Staphylinidae and Araneae to reach comparable densities within the beetle bank to those in the field margins, may have been attributed to the different dispersal mechanisms employed by these taxonomic groups and also changes in the vegetation structure of the beetle bank. Many species of Staphylinidae such as those belonging to the genus *Tachyporus* disperse by flying. Immature Linyphiidae and Lycosidae as well as some adult linyphiids also disperse aeronautically by a process known as 'ballooning' (Roberts, 1995). The Staphylinidae and Araneae are therefore capable of dispersing long distances (many kilometres in the case of the Linyphiidae (Halley *et al.*, 1996)), over short periods of time, when locating overwintering or alternative habitats. Conversely the majority of Carabidae found overwintering in field boundary habitats, possess limited powers of dispersal and although some can fly over short distances, others are capable only of walking (Coombes & Sotherton, 1986). Therefore it may have taken longer for the Carabidae to encounter and colonise the beetle bank.

Tussock forming grass species such as *Dactylis glomerata* and *Holcus lanatus* have long been associated with supporting high densities of overwintering invertebrates (Luff, 1966). It has been suggested that the microclimate within tussocks during winter months, increases the chances of invertebrate overwintering survival (Bossenbroek *et al.*, 1977). Temperatures within tussock forming grass species during the winter are less variable than those in species with loose or mat-like growth forms (Luff, 1966; Bossenbroek *et al.*, 1977; Thomas *et al.*, 1992a). The less variable temperatures found within tussock forming plant species are attributed to the height and density of the vegetation. The level at which radiation is absorbed increases as the height and density of the vegetation increases. This in turn reduces temperature fluctuations in the lower parts of the vegetation (Luff, 1965). From seed *D. glomerata* takes at least three years to mature and during this time dead leaf material accumulates at the base of the tussock (Luff, 1965). The height of *D. glomerata* also increases over time as seen from the results of this experiment. Therefore as the height and density of a tussock increases with age so does its capacity to maintain stable

temperatures (Luff, 1966), which in turn aids the overwintering survival of invertebrates (Desender, 1982). Several workers have concluded that the structure of tussocky vegetation, in particular the biomass of living and dead grass, does act as an important stimulus in the process of overwintering site selection, for the carabid *Demetrias atricapillus* and members of the genus *Bembidion* (Bossenbroek *et al.*, 1977; Andersen, 1985; Thomas *et al.*, 1992a). Although tussock biomass was not investigated in this study, there was an observed increase in tussock density over the study period, which could also explain the later arrival of many carabid species on the beetle bank.

The hedgebanks were dominated by *Elytrigia repens*. Lagerlöf and Wallin (1993) found that *E. repens* supported high densities of overwintering polyphagous predators. They showed that when this grass species was removed from field margins catches of polyphagous predators were reduced. These workers concluded that this reduction was attributed to both the disappearance of the dense vegetation and the deep sod layer associated with *E. repens*. Positive correlations between the depth of the sod layer and numbers of overwintering Staphylinidae and Carabidae have been recorded (Desender, 1982; D'Hulster & Desender, 1982: D'Hulster & Desender, 1984). *E. repens* occurs commonly in hedgebanks and is considered to be an agricultural weed (Marshall, 1988). Although the development of herbicides such as glyphosate has meant that *E. repens* poses less of a problem to farmers, it would not be advisable to use this species as overwintering cover for polyphagous predators on beetle banks. Overall hedgebank 2 was particularly noticeable in supporting high densities of polyphagous predators. The soil in this long established hedgebank appeared to be particularly well aerated and drained compared to hedgebank 1 and the beetle bank which was probably attributed to the well developed organic/humus layer. Dennis *et al* (1994) found higher densities of *Tachyporus hypnorum* and other beneficial predators in field boundaries with lower soil moisture content. The soil on the beetle bank was of a heavy clay type and was prone to becoming saturated in wet weather during the winter. In the winter of 1997 wet weather persisted and this may have made the beetle bank less favourable as a site for overwintering polyphagous predators. The vertical distribution of polyphagous predators within the vegetation and soil layers in the beetle bank and hedgebanks also differed. The majority of predators found overwintering in the beetle bank were found buried deep within the tussocks and in the sod layer, predators were rarely found in the clayey soil. Conversely the predators overwintering in the hedgebanks were often found overwintering in the soil particularly in

the humus layer. Again this was probably attributed to different soil types in these habitats and their soil moisture content.

Differences in the percentage ground cover of vegetation in the beetle bank and hedgebanks may have influenced the distribution of overwintering Lycosidae, which were more abundant on the beetle banks compared to the hedgebanks. Unlike the Linyphiidae, which remain active during the winter, overwintering passively only when temperatures fall below -4 ^{0}C (Foelix, 1982), personal observations indicated that the Lycosidae were less active and were found overwintering particularly within the tussocky vegetation on the beetle bank. Bayram and Luff (1993) also found high densities of overwintering Lycosidae in tussock forming grasses and suggested that these spiders may actively select grass tussocks in which to overwinter. The percentage cover of tussocky vegetation was greatest on the beetle bank compared to the hedgebanks, which may explain why the beetle bank appeared to be a more favourable habitat for this family. However the results from this study should be viewed with caution, as numbers of Lycosidae caught were low. Nevertheless Maelfait and De Keer (1990) also found that the lycosid *Pardosa amentata* is closely associated with border zones/field margins and suggested that this reflected the need for overwintering sites for juveniles of this species. They concluded if these sites were not available, species such as *Pardosa amentata* would not exist in agricultural fields. Therefore beetle banks may provide a particularly important habitat for this family. The linyphiid on the other hand may be less reliant on tussocky grass species for overwintering habitats. Bayram and Luff (1993) found that linyphiids showed no preference between tussock and non-tussock forming grasses indicating that this family may have considerable cold-hardiness compared to the Lycosidae. Overall linyphiid density was similar in the beetle banks and hedgebanks.

Thomas *et al.* (1992b) reported an increase in the proportion of Lycosidae to Linyphiidae from a beetle bank's initial establishment over a three year period in Hampshire. They concluded that this was a successional process from pioneer/r-strategist species (ie. linyphiids) which exploit newly created or disturbed habitats, where competition is low, to K-strategist species (ie. lycosids) which colonise more permanent and specialised habitats. However MacLeod (1994) who continued the study by Thomas (1991) for a further four years described an increasing dominance of the Linyphiidae within the beetle banks in Hampshire from the fourth year onwards. There was little evidence of an increase in the

proportion of Lycosidae to Linyphiidae overtime on the beetle bank in this study, although the low numbers of spiders caught made any trends difficult to determine. This, coupled with the Linyphiidae dominating the two well established hedgebanks in Leicestershire, may somewhat discount the successional theory. Agricultural habitats are continuously changing and organisms are disturbed by farming operations such as rotational cropping. Araneae that are best adapted to these environments are those with r strategist adaptions, such as the Linyphiidae which can escape ploughing and pesticides by ballooning and which produce two or more generations per year (Maelfait & De Keer, 1990; Duffey, 1993; Halley *et al.*, 1996; Topping & Sunderland, 1998). Therefore it is not surprising that the Linyphiidae are considered to be the most abundant family of spiders found within cereal crops in the UK (Sunderland *et al.*, 1986) and that they are found in equal or greater proportions to Lycosidae in overwintering sites.

Within the agricultural industry it is common practice for farmers to annually cut vegetation in field margins. A recent study by Baines *et al.* (1998) showed that Araneae species richness and abundance was positively correlated with vegetation height. They showed that when vegetation was cut to a height of 4-5 cm Araneae species richness and abundance was reduced. Structural complexity has been shown to favour an increase in Araneae diversity, as spatial segregation is one way in which Araneae may partition habitat resources (Robinson, 1981). The overall effect of autumn cutting on winter active or winter adult Araneae is unknown and deserves further investigation. However cutting during the autumn/winter period will affect the structure of tussock forming grass species and this will have a detrimental effect on the ability of the tussock to maintain stable temperatures. Therefore cutting may not only affect the Araneae but also other overwintering predators. However leaving field margins uncut for more than two years can lead to scrub encroachment (Smith *et al.*, 1993). Baines *et al* (1998) suggested that structural diversity could be preserved during field margin management by employing some form of rotational cutting whereby some areas of tall swards are left untouched whilst other areas are cut back. Scrub encroachment may also become a problem on beetle banks as they age and a similar method of management could be employed to prevent this.

Whether the importance of overwintering sites for Linyphiidae is a key factor in their survival is unknown, although some species have been recorded migrating from fields to field margins during the winter, possibly for overwintering purposes (Maelfait & De Keer,

1990). However beetle banks, hedgebanks and other non-cropped habitats are particularly important refugia for the Linyphiidae when crops are sprayed with insecticide. Aebischer & Potts (1990), studied Linyphiidae abundance over a 20 year period and found that abundance declined at a rate of 4.1 % per year in a period of increased insecticide use, when synthetic pyrethroids to which linyphiids are particularly susceptible, were introduced. Halley *et al.* (1996) also found that the inclusion of small amounts of grassland in large areas of cereal production dramatically increased the population of spiders in the landscape. Many species of Araneae including Linyphiidae found within the beetle bank in this study prey on cereal aphids. For example, the linyphiid *Bathyphantes gracilis* and lycosids species belonging to the *Pardosa* (Sunderland *et al.*, 1986 &1987a; Nyffelen & Benz, 1988; Janssens & De Clercq, 1990). Therefore even if overwintering sites for Linyphiidae are not a key factor in their survival, beetle banks may act as important source of this family for the biological control of cereal aphids. This is particularly important as new evidence has indicated that although linyphiids can balloon many kilometres, wind conditions usually only allow dispersal over short distances of a few metres at any one point in time (Suter, 1999 in press).

Once established within the beetle bank densities of overwintering Carabidae, also remained at levels comparable to or greater than those found in the field margins. During the study period the proportion of 'boundary' type carabids to 'open-field' type carabids increased in the beetle bank. Thomas *et al.* (1992b), also described this change as succession, as with the Araneae. MacLeod (1994), however suggested these changes were attributable to a temporal rather than successional process ie. the longer a beetle bank stays in position, the greater the probability that 'boundary' type Carabidae locating an overwintering site will encounter the bank. In conclusion, both temporal and successional processes may influence the carabid community structure over time as conditions within the beetle bank may take several years before becoming favourable to 'boundary' type Carabidae locating an overwintering site, as discussed previously.

Twenty one species of carabid were identified within the beetle bank over the five year period, the majority of which were common to beetle banks both in Leicestershire and Hampshire. By the end of the study species composition in the hedgebanks and beetle bank was similar. One of the dominant carabid species found during the study in Leicestershire, was *Demetrias atricapillus*. This species was common on the beetle bank

and is also a member of the 'highly ranked boundary carabids'(Sotherton 1984). Species belonging to this group require boundary type habitats in which to overwinter and have also been ranked highly as aphid predators by Sunderland & Vickerman (1980). Many Carabidae including *D. atricapillus*, which is ranked as the most important aphid predator in the group 'highly ranked boundary carabids', disperse by walking. Without the beetle bank these species would have to disperse further in order to reach the centre of cereal fields during the summer. In turn these predators fully colonise fields more quickly, which is particularly important as manipulative experiments have shown that predation by polyphagous predators is most effective during the early stages of aphid establishment (Edwards *et al.*, 1979; Chiverton, 1986).

The staphylinids *Tachyporus hypnorum* and *Tachyporus chrysomelinus* have also been ranked highly as cereal aphid predators and have been found overwintering in field boundaries (Sotherton, 1984; Sunderland & Vickerman, 1980; Dennis *et al.*,1990; Dennis & Wratten, 1991). *T. hypnorum* dominated the *Tachyporus* species throughout the study and was abundant within the beetle bank from the second winter, when sampling first took place. Densities of *T. hypnorum* and *T. chrysomelinus* were comparable to or greater than those within the field margins throughout the five year period. *Tachyporus* species are able to fly and can disperse rapidly throughout a crop in the spring (Thomas, 1991).

Overall the Staphylinidae dominated the total catch of overwintering predators within all the habitats throughout the study. Several staphylinids apart from *Tachyporus hypnorum* and *Tachyporus chrysomelinus* have been found to prey on cereal aphids these include *Philonthus cognatus*, Omaliinae spp, Oxytelinae spp, Steninae spp, Staphyliniae spp and other Tachyporniae spp such as *Tachyporus obtusus* (Sopp & Wratten, 1986; Dennis & Wratten, 1991; Good & Giller, 1988 & 1991; Andersen, 1992; Kross & Schaefer, 1998). With the exception of *Tachyporus hypnorum* and *Tachyporus chrysomelinus* species belonging to the above taxa were rarely encountered during the study in Leicestershire. The most dominant staphylinid species found during the study belonged to the genus Aleocharinae. Aleocharinae species were found not to react positively to an ELISA test with cereal aphid antiserum (Sunderland & Vickerman, 1980), but Sunderland *et al.* (1987a) suggested they should not be dismissed as cereal aphid predators. During May-June Aleocharinae species are abundant in cereal fields (Andersen, 1982; pers. obs.) and may therefore be of significant importance. These and other Staphylinidae deserve further

investigation. Without the beetle bank high densities of potentially beneficial predators (in particular those that disperse by walking) would not be present at field centres during the winter, ready to disperse into the crop during spring.

The most apparent change in the vegetational composition of the beetle bank, during the study, was the dominance of *Dactylis glomerata* over *Holcus lanatus*. By the winter of 1994, the third winter of the beetle bank's development, *H. lanatus* was virtually non-existent and persisted only at the edges of the bank, whilst *D. glomerata* dominated the rest. Therefore it is not advisable to sow mixtures of these two grasses on beetle banks, particularly as seed for *H. lanatus* is expensive and difficult to obtain. The competitiveness of *D. glomerata* prevented the invasion of weed species. During the study, there were no agronomic problems associated with the beetle bank, in terms of invasion into the crop by the grass species sown on the bank.

Densities of Araneae, Staphylinidae and Carabidae found within the beetle bank in Leicestershire during the second and third winters, were compared to those found by Thomas *et al.* (1992b) in *D. glomerata* treatments within a beetle bank of the same age in Hampshire. The Hampshire bank bisected a similar sized field (20 ha) to the one in Leicestershire (18ha).

Carabid density within the bank in Leicestershire during the second year, was comparable to that in Hampshire (40 m^{-2} & 97 m^{-2} respectively). During the third winter densities were greater in Hampshire than Leicestershire (241 m^{-2} & 80 m^{-2} respectively). Carabid density in Leicestershire did not reach particularly high densities until the fourth winter (301 m^{-2}), of the beetle bank's existence. Staphylinidae densities within the beetle bank in Leicestershire were greater than those in Hampshire in the second (505 m^{-2} & 69 m^{-2} respectively) and third (377 m^{-2} & 182 m^{-2} respectively) winters. The Araneae were not sampled from the beetle bank in Leicestershire in the second winter, but were comparable to those in Hampshire in the third winter (136 m^{-2} & 130 m^{-2} respectively).

There is still the question as to whether beetle banks actually enhance predator populations at the field centre or whether there is simply a redistribution of existing populations within the field (Thomas *et al.*,1991)? This is a very difficult question to answer. During this study it was found that the density of Carabidae with low powers of dispersal remained

stable over the five year period in the surrounding hedgebanks, whilst densities in the beetle bank increased. However, it is difficult to distinguish between short term fluctuations and long term increases and decreases in density within the field boundaries and beetle bank. Predator populations may have to be sampled with increased intensity over a longer period of time before this question can be fully answered.

Beetle banks could also potentially harbour high densities of overwintering pest species in particular *Sitobion avenae*. However no aphids were recorded overwintering on the beetle bank or in the hedgebanks in this study.

The standard errors of the means of the numbers of polyphagous predators found in the soil cores, were quite large, throughout the study. This was partly due to low catches of some species and patchy distributions of others. For example, certain species such as *Demetrias atricapillus*, aggregate in large numbers particularly within grass tussocks during the winter (Thomas *et al.*, 1991; personal observation). By increasing the sample size from a given habitat, these problems may be resolved. It was estimated in this study that a sample size of approximately 120 cores from each site, would be needed to reduce the standard error to an acceptable level. However soil coring is labour intensive and time consuming and a sample size this large may not always be practical. Large sample sizes may also disrupt a habitat, as soil coring is a destructive technique. Several non-destructive techniques for sampling overwintering invertebrates have also been tested, for example surface searching and vacuum samples, but these methods have proved unsatisfactory compared to soil coring (Dunkley, 1997). The optimum number of soil cores per habitat will depend on a variety of factors such as habitat size. Therefore it is advisable to carry out some preliminary sampling before starting a major project.

In conclusion, this study along with evidence from beetle banks in Hampshire (Thomas *et al.*, 1991 & 1992b; MacLeod 1994) has shown that beetle banks can provide adequate overwintering resources for polyphagous predators, by the second year of the bank's creation, with densities of some of the most beneficial invertebrates similar to or greater than those found in conventional field boundaries. Beetle banks are particularly important for maintaining high densities of overwintering predatory species, that disperse by walking and which have been ranked highly as aphid predators. Where a beetle bank is present in conjunction with well maintained field margins, predators that disperse by walking should

have the ability to fully colonise a large field earlier in the spring than they would do otherwise. This would enable these predators to prey on aphids in the establishment phase, thus potentially preventing an aphid outbreak. This theory was tested in the experiment described in chapter 3.

2.4.2 Assessment of overwintering habitat preference for different grass species

This study revealed that the density and composition of overwintering polyphagous predators within the six treatments differed significantly over the four year study period. Two grass species namely *A. elatius* and *D. glomerata* were highlighted as providing the most suitable overwintering habitat for polyphagous predators overall. Conversely the natural regeneration treatments proved to be the least suitable habitat for overwintering polyphagous predators.

Overall total predator density increased between 1994 and 1996, with peak predator density recorded in 1996. Densities of the individual taxonomic groups, fluctuated between years within each of the different grass treatments. However, the overall peak densities of the 'highly ranked boundary type Carabidae', 'boundary type Carabidae', Araneae and *Tachyporus* species and were recorded in 1996. Peak staphylinid and carabid densities were recorded in 1995. These results are similar to those recorded in the first experiment detailed in this chapter (section 2.3.1), where peak predator densities were recorded in 1996. This indicates that similar factors were affecting predator population density within the beetle banks, in both experiments. Examples of these are discussed in section 2.4.1.

Total polyphagous predator density was greatest in the tussock forming grasses *A. elatius*, *D. glomerata* and *P. pratense*. The highest density was recorded in *A. elatius* which was primarily due to the large proportion of Staphylinidae found overwintering in this grass treatment. The Staphylinidae were the dominant taxonomic group contributing to the total in all the treatments and as indicated above staphylind density was generally greater in these three tussock forming species. The least favourable treatments were the natural

regeneration treatments and to a lesser extent the *C. cristatus* treatments. As mentioned in the previous discussion (section 2.4.1) several staphylinid species prey on aphids including *T. hypnorum* which dominated the Staphylinidae throughout the study. *T. hypnorum* along with *T. chrysomelinus* which made up the group '*Tachyporus* species' were common in all the treatments, but there were no clear indications as to which treatment provided the best overwintering cover. However the highest densities were again recorded in *A. elatius*. As in the first experiment detailed in this chapter (section 2.3.1) the Aleocharinae were also abundant on the beetle banks whereas other aphid eating species excluding the *Tachyporus* species were less numerous.

Total carabid , 'boundary' type carabid and 'highly ranked boundary carabid' density was significantly greater in the *D. glomerata* treatments compared to any other treatment. *D. glomerata* supported particularly high densities of *Demetrias atricapillus* the most important carabid in the 'highly ranked boundary carabids'. Thomas *et al.* (1992b) also recorded high densities of this carabid in *D. glomerata* on beetle banks in Hampshire. This information is particularly important because many of the 'highly ranked boundary carabids' such as *D. atricapillus* disperse into the crop from overwintering habitats during spring by walking (Coombes & Sotherton, 1986). One of the main functions of a beetle bank is to aid the dispersal of these carabids throughout crops during the spring, before the onset of an aphid invasion. Therefore it is imperative that conditions preferred by these species are present on beetle banks. As for the Staphylinidae the highest carabid densities with the exception of *D. glomerata* were recorded in the tussock forming grasses. The least favourable treatments were the natural regeneration and *C. cristatus* treatments.

Araneae density was greatest in *D. glomerata*, *A. elatius*, *C. cristatus* and *P. pratense*, and to a lesser extent in the *F. rubra* treatments. The lowest densities were again recorded in the natural regeneration treatments. However all the treatments supported Araneae which have been found to prey on aphids. Although Araneae density was generally greatest in the tall growing tussock forming species, densities were also surprisingly high in the non-tussocky *C. cristatus* treatments. Several other studies have also found that Araneae densities are greatest in tussock forming species compared to non-tussock forming grass species, though not always significantly (Thomas *et al.*, 1992b; McLeod, 1994). No significant differences were recorded for the Linyphiidae and Lycosidae between the treatments. However the Linyphiidae and Lycosidae were generally more abundant in the

taller growing treatments compared to those dominated by lower growing vegetation namely the natural regeneration and *F. rubra* treatments. Habitat site selection by the Araneae may be influenced by biotic as well as abiotic factors. Thomas *et al.* (1992a) showed that a suitable food source was an important requirement for the carabid *Demetrias atricapillus* and the staphylinid *Tachyporus hypnorum*. These two species do not enter an obligate diapause in the winter, with periods of activity/inactivity influenced by environmental factors (Coombes, 1987). As mentioned in the previous discussion (2.4.1) Linyphiidae are active during winter even at very low temperatures (Foelix, 1982) and presumably require food during this period. Winter activity by the Lycosidae, presumably foraging for food, has also been recorded at temperatures as low as 0.5 ^{0}C, particularly in sunny conditions (Bayram & Luff, 1993). Whether differences in prey density occurred between the treatments is unknown but research has shown that higher prey densities are associated with taller and more structurally diverse vegetation (Southwood *et al.*, 1979; Hawthorne & Hassall, 1995). This may therefore partially explain some of the observed trends detailed above. In conclusion further research is needed to investigate the overwintering requirements of the Araneae. As discussed previously (section 2.4.1) the dependency on overwintering sites may not be the same for the Lycosidae and Linyphiidae or even for individual species in these two sub-families. By increasing the number of soil cores taken from each treatment significant differences between treatments for these sub-families and species may be found, providing a greater understanding of their overwintering needs. However because plot size was relatively small, an increase in sample size may cause significant disruption to the vegetation in the treatments.

These results reflect findings by other researchers that tussocky grass species, in this case *A. elatius* and *D. glomerata*, and to a lesser extent *F. rubra* and *P. pratense*, provide particularly important refugia for overwintering polyphagous predators (Luff, 1966; Thomas *et al.*, 1991; MacLeod, 1994). *C. cristatus* does not form tussocks and the natural regeneration treatments were dominated by non-tussocky vegetation. With the exception of the Araneae these two treatments, in particular the natural regeneration treatment, generally supported lower densities of polyphagous predators compared to the other treatments. As mentioned in the previous discussion, vegetation height affects the rate of absorption of radiation by plants, thus influencing a plant's ability to maintain stable temperatures in winter. Compared to *A. elatius*, *D. glomerata* and *P. pratense*, *F. rubra*

and *C. cristatus* are lower growing species as was the vegetation in the natural regeneration treatments. Therefore it is not surprising that the latter two species in particular supported lower densities of predators. The tussocky structure of *F. rubra* could compensate for its lack of height and therefore this species may be more suitable for overwintering Carabidae and Staphylinidae, compared to *C. cristatus* and the natural regeneration treatment.

Densities of Staphylinidae and Carabidae found within the *D. glomerata* treatments in Leicestershire over the four year period were compared to those found by MacLeod (1994) in *D. glomerata* treatments within a beetle bank of the same age in Hampshire. The bank in Hampshire bisected a similar sized field (7.3 ha) to the one in Leicestershire (8.6 ha). Overall carabid density was greater within the *D. glomerata* treatments in Hampshire compared to those in Leicestershire. However carabid density in the fourth year in Leicestershire did exceed that in Hampshire (596 m^{-2} & 138 m^{-2} respectively). Staphylinid density on the other hand was greatest overall in Leicestershire, with the exception of the fourth year when densities were greater in Hampshire.

In the final years of MacLeod's (1994) study, he also investigated the grasses *A. elatius* and *F. rubra* which were sown on the same beetle bank as above. Results for these two grasses were only available for the second and third years of their establishment. Therefore it was only possible to compare the results from Leicestershire over the same time period. Overall carabid densities within the *A. elatius* and *F. rubra* treatments in Hampshire exceeded those in Leicestershire. However carabid density in the third year in the *A. elatius* treatment in Leicestershire was similar to that in Hampshire in the third year (257 m^{-2} & 396 m^{-2} respectively). Staphylinid densities were greater overall in the *A. elatius* treatments, but lower in the *F. rubra* treatments in Leicestershire compared to those in Hampshire.

It is difficult to make comparisons between beetle banks at two different geographical locations because factors such as previous insecticide regimes, may affect the number of polyphagous predators available to colonise beetle banks. However, the staphylinid and carabid densities at these two locations were not too dissimilar in the above treatments and both MacLeod (1994) and Thomas *et al.* (1991 & 1992b) found that tussocky grass species provided the best overwintering cover for these families.

The results from this experiment and others like it, (Luff, 1966; Thomas *et al.*, 1991, 1992a & 1992b; MacLeod, 1994) have provided some insight as to which grass species should be recommended for sowing on beetle banks. As discussed before, beetle banks are particularly important for those species of polyphagous predator, that require boundary type habitats as overwintering refugia and which disperse by walking. These predators are mainly incorporated within the 'boundary type' Carabidae and the Carabidae within the group 'highly ranked carabid species' (eg. *Demetrias atricapillus* & *Bembidion lampros*). *D. glomerata* provided the best habitat for these carabids and other predators such as the Araneae. This grass species is therefore highly recommended for sowing on beetle banks. Thomas *et al.* (1991 & 1992b) and McLeod (1994) also recommended that this grass species be sown on beetle banks.

A. elatius also supported high densities of overwintering polyphagous predators, but seed for this species is more expensive and is not as easily available as it is for the other four grasses. However this form of *A. elatius* is commonly found growing in hedgerows and field margins, and should be actively encouraged where it is found growing naturally.

Although leaving beetle banks to naturally regenerate would be the cheapest option, the results from this experiment would not recommend this. There is also the potential for the banks to become dominated by weed species if they are left to naturally regenerate, hence posing an agronomic problem to the farmer.

Bare patches of ground were often observed throughout the study, around the tussocks of *D. glomerata* and *A. elatius*, particularly during winter. Bare ground is not suitable as an overwintering site for many predators, in particular boundary type Carabidae, as little protection is provided against temperature fluctuations and other environmental factors (Chiverton, 1989; Thomas *et al.*, 1992a). To provide extra overwintering cover for predators, another grass species such as *F. rubra* could be sown along with these tussocky species. In experiments not detailed in this study, *F. rubra* was found to grow well in a mixture with *D. glomerata*, but not so well in a mixture with *A. elatius*. Similar results were found by Grubb (1982) in an eight year study of plots sown with mixtures of either *A. elatius* or *D. glomerata*, with *F. rubra*. A potential problem regarding the grasses sown on the beetle banks, could be damage by spray drift from applications of graminicides to

crops. A residual herbicide-treated strip/buffer zone between the beetle bank and the crop would minimise drift, but would lead to further land being taken out of production (Sotherton, 1995; Wratten & Van Emden, 1995). An added advantage of *Festuca* species is that they are resistant to many graminicides (Marshall & Nowakowski, 1991). *F. rubra* also has a creeping habit and colonises bare ground preventing invasion by weed species. This experiment showed that *F. rubra* provided a suitable habitat for polyphagous predators, in particular 'highly ranked boundary carabids'.

Mixtures of *D. glomerata* or *A. elatius*, with either *P. pratense* or *C. cristatus*, have not been investigated in this study. However *C. cristatus* was found to be out competed by other species in this experiment and would probably not perform well in a mixture with either of the two competitive tussocky grasses. Mixtures of *P. pratense*, *D. glomerata* and *F. rubra* on beetle banks in Sweden, have shown promising results in terms of polyphagous predator densities in first winter of the grasses establishment (Chiverton, 1989). Another advantage of the tussocky grass species *P. pratense*, *F. rubra* and *D. glomerata* are that they are cold hardy, and are therefore particularly useful for sowing on beetle banks in more northerly latitudes, such as Sweden and Denmark (Chiverton, 1989; Sotherton, 1995).

Mixing grass species may also inadvertently benefit the Carabidae and Araneae. Several studies have shown that vegetational structural complexity is positively correlated with the abundance and diversity of these two families (Robinson, 1981; White & Hassall, 1994; Hawthorne & Hassall, 1995; Baines *et al.*, 1998). This may be attributed to greater prey abundance in taller growing more structurally diverse environments (Hawthorne & Hassall, 1995). By increasing the structural complexity of vegetation on the beetle bank prey abundance may be enhanced, which could increase the survival of winter active Araneae and carabids that do not enter obligate diapause during winter (Thomas *et al.*, 1992a). Structural complexity also enables a greater number of Araneae to utilise the same resource. For example many species of web building Araneae require specific web building sites (Baines *et al.*, 1998), such as *Bathyphantes gracilis* and *Lepthyphantes tenuis* which prefer to build webs 10 cm above the ground (DeKeer *et al.*, 1989; Alderweireldt, 1994a). By increasing the abundance and diversity of Araneae and Carabidae on beetle banks via an increase in the structural complexity of the vegetation, beetle banks may be improved as a source of aphid eating predators.

In conclusion *D. glomerata* appears to be the most suitable grass species for growing as a single stand on beetle banks. Seed for this species is cheap and easy to obtain, and once the grass has established it is also easy to maintain. Mixtures of *D. glomerata* with other grass species warrants further investigation, to observe whether the greater availability of overwintering cover and an increase in structural diversity, actually enhance predator populations on beetle banks.

2.5 SUMMARY

Two main conclusions can be drawn from the studies of overwintering predator densities on beetle banks in Hampshire (Thomas *et al.*, 1991 & 1992b; McLeod, 1994) and Leicestershire. These are: i) beetle banks provide a suitable habitat for overwintering polyphagous predators, with densities similar to or greater than those in surrounding field margins and ii) tussocky grass species, in particular *Dactylis glomerata* and *Arrhenatherum elatius*, support the highest densities of overwintering polyphagous predators.

However several points have been highlighted by these experiments that require further consideration.

- The initial colonisation of a beetle bank by polyphagous predators may be affected by several factors including; the size of the field, summer densities of predators within the field which is influenced by crop and cultivation type, previous insecticide regime and quality of the surrounding field margins (Sotherton, 1984 & 1985; Asteraki *et al.*, 1992; Booij & Noorlander, 1992; Purvis & Bannon, 1992; Thomas & Marshall, 1999). Thomas *et al.* (1992b), studied three beetle banks in Hampshire which bisected fields of different sizes. They found that carabid density was lowest in the beetle bank which bisected the largest field (51 ha compared to 7 ha & 20 ha). This was attributed to the size of the field and an impoverished carabid fauna which may have resulted from the previous severe insecticide regime carried out in that field. As discussed previously, those predators that disperse by walking (eg. many species of Carabidae), may take

longer to encounter a beetle bank in a large field compared to those predators that disperse by flying. This raises the question as to whether more than one beetle bank should be created in fields of 50 ha or more.

The beetle banks detailed in this chapter were situated on an estate where policies are adopted to increase invertebrate food availability for gamebird chicks. For example insecticides are only used in summer when pests are above threshold, and if they are used more selective chemicals are employed. Also no applications of insecticide are applied to the outer 6-12 metres of crops and field margins are well maintained. Where there have been no previous policies adopted to encourage invertebrate fauna, the colonisation of a beetle bank by predacious invertebrates may be impaired (Thomas *et al.*, 1992b). This in turn will adversely affect the role of the beetle bank in a biological control regime.

- It is not known whether beetle banks actually enhance predator populations in cereal fields, or whether predator populations are simply redistributed within the field. Although this question was discussed previously (section 2.4.1) it still remains to be fully answered.

- The longevity of beetle banks is unknown, i.e. does the ability of a beetle bank to support high densities of predators diminish after a certain period of time. As discussed previously (section 2.4.1), changes in the development of grasses sown on beetle banks may affect predator population density within a beetle bank. Luff (1965) found that the accumulation of dead leaves begins to choke the new growth of *D. glomerata* after approximately 7 years. After 8 to 10 years *D. glomerata* loses its competitive ability and other plants start to invade. A recent study has indicated that there is a negative relationship between the percentage cover of tussocks on beetle banks and age of beetle banks (S. Thomas, pers. comm.). Overwintering polyphagous predator densities on beetle banks have only been studied over relatively short periods of time, the longest being 7 years in the case of one beetle bank in Hampshire (McLeod, 1994). To answer the above question, long-term ecological studies of beetle banks, spanning more than 10 years are required. However the comparable numbers of predators found in the hedgebanks in this study indicate that provided sufficient densities of appropriate grasses are maintained then their value should not depreciate

with time. Some form of management may also be required to prevent scrub encroachment on beetle banks. A management system similar to that described by Baines *et al.* (1998) for field margins could be applied as discussed in section 2.4.1.

- It is still not known whether the provision of an overwintering resource is a key factor (Varley & Gradwell, 1960) in the life cycle of these predators. For example, between-year fluctuations in the numbers of farmland Carabidae may be most influenced by larval mortality in the crop in the summer (Wratten and Van Emden, 1995).

- It is important to take into consideration any knowledge about the biology of overwintering invertebrates, when interpreting any results about predator population densities. Thomas *et al.*, (1991 & 1992b) found that total predator density peaked (1500 m^{-2}) after only two winters within *D. glomerata* treatments sown on a beetle bank in Hampshire. This finding led researchers to publicise the technique for creating beetle banks, which subsequently resulted in a great deal of media attention (McLeod, 1994). However a density of this magnitude was not sustained or attained after the second winter (McLeod, 1994). On further investigation it was found that the high density recorded in the second winter was attributed to a particularly high density of *Demetrias atricapillus* (922 m^{-2}). *Demetrias atricapillus* was found by Thomas *et al.* (1991) to aggregate in large numbers within the tussocks of *D. glomerata*, resulting in rather a patchy distribution of this species on the beetle bank. The sampling method employed by Thomas *et al.* (1991 & 1992b) was similar to that used in the experiments detailed in this experiment. By increasing the sample size from a given habitat, the problem of patchily distributed organisms may be resolved (section 2.4.1). However soil coring is labour intensive and time consuming, therefore it may not be feasible to greatly increase sample size. Therefore it is vitally important to interpret data carefully when investigating predator population density over time.

- Finally, since Thomas *et al.* (1991& 1992b) work in the early 1990s, beetle banks have been promoted throughout the UK (and abroad) by The Game Conservancy Trust and The Ministry of Agriculture, Fisheries and Food (MAFF). Farmers are now eligible for a grant of £15/100m/year for beetle banks and grass margins under the Countryside Stewardship Scheme (MAFF, 1996 & 1999a). MAFF have also piloted a new Arable Stewardship Scheme to assist the recovery of farmland plants and animals in

Shropshire and South Cambridgeshire/West Suffolk (MAFF, 1998c). This scheme also includes beetle banks under its options. These two organisations have promoted beetle banks as playing a potentially important role in Integrated Pest Management programmes. However there is little evidence to date of the agronomic benefits of beetle banks. For example, although beetle banks have been shown to support 'high' densities of polyphagous predators there is little evidence that predators arising from the beetle bank can suppress aphid populations maintaining their numbers below set economic thresholds. The next chapter in this thesis will assess the impact of beetle banks on aphid populations in winter wheat.

CHAPTER 3.

THE INFLUENCE OF BEETLE BANKS ON CEREAL APHID PREDATION IN WINTER WHEAT

3.1 INTRODUCTION

During the spring and summer cereal aphids cause direct damage to winter wheat, which can result in reduced yields and grain quality (Lee *et al.*, 1981; Holmes, 1984; Oakley & Walters, 1994). Since the 1970s substantial evidence has accumulated about the potential of polyphagous predators to control aphid populations, within cereal crops. Predator exclusion experiments have shown that polyphagous predation is most important during early spring, when aphid populations are establishing and predator-prey ratios are high (Edwards *et al.*, 1979; Chiverton, 1986). Confirmation of polyphagous predation during the aphid establishment phase has come from ELISA tests and gut dissections, which have highlighted key polyphagous predator species important in controlling aphid populations (Sunderland & Vickerman, 1980; Sopp & Wratten, 1986; Sunderland *et al.*, 1986; Chiverton, 1987; Sunderland *et al.*, 1987a).

However, there has been a decrease in polyphagous predator abundance on farmland since the 1970s, which has been linked to the intensification of farming practices over this period, involving hedgerow removal to create larger fields and the use of broad-spectrum insecticides (Aebischer & Potts, 1990; Aebischer, 1991; Sotherton, 1995). Recently attitudes towards the environment have changed and the efficiency and cost-effectiveness of the prophylactic use of pesticides in crop protection has been questioned (Greig-Smith, 1992), particularly as grain prices continue to fall and farmers are seeking ways in which to reduce inputs. This has stimulated interest into 'integrated crop management' in which the control of crop pests by natural enemies is encouraged. It has been suggested that by creating beetle banks, thereby augmenting polyphagous predator numbers in the centres of cereal fields and reducing the distance they have to disperse in order to reach the field centre, cereal aphid populations can be controlled (Thomas *et al.*, 1991). Although beetle banks have been shown to support 'high densities' of overwintering polyphagous predators (Thomas *et al.*, 1991 & 1992b; McLeod, 1994; Collins *et al.*, 1996) it is still not known whether these predators dispersing from the beetle bank in the spring can reduce aphid numbers in the crop. This experiment aimed to investigate the impact of the creation of a beetle bank on the grain aphid *Sitobion avenae*, which is the species that most frequently causes direct damage to winter wheat in the UK (Dent, 1995). Polyphagous predator densities were manipulated using exclusion barriers placed at set distances away from the

beetle bank to assess the impact of predators emigrating from the bank on populations of *Sitobion avenae*.

3.2 MATERIALS AND METHODS

3.2.1 Study site

The study was undertaken in an 18.3 ha arable field (Grid ref SK 796 020) on the Loddington Estate, Leicestershire. A 400m long beetle bank (2.5m wide x 0.5m high), sown with a mixture of the grass species *Dactylis glomerata* and *Holcus lanatus* during spring 1992 separated the field into two halves (as described in section 2.2.1.1.). The northern half of the field (7.48ha) was used and was sown to winter wheat cv. Riband.

3.2.2 Creation of the enclosures

The field was divided into four 100m long blocks, within each block 'predator-reduced' areas and control areas were positioned at random at four fixed distances away from the beetle bank. In each block the first treatment was placed 8m from the beetle bank and the remainder were placed at 25m intervals (Fig. 5). On the 15 April 1996 predator-reduced areas were created using polythene enclosures (7x8m) which were buried approximately 15cm into the ground using a tractor mounted barrier laying machine, to form a barrier approximately 45cm high (Plate 2). The enclosures were designed to exclude ground dwelling predators only (Plate 3). The controls consisted of similar areas marked out with canes but with no exclusion barriers, allowing free movement of invertebrates.

3.2.3 Monitoring of *Sitobion avenae* numbers within the enclosed and control areas

On the 21 June 1996, 75 laboratory reared *Sitobion avenae* (obtained from the Central Science Laboratory, Harpenden, Herts) were placed on twenty ears of wheat, in each experimental area. To minimise the microclimatic effects of the polythene lining, tillers were randomly chosen at least one metre away from the polythene barrier. Each tiller was tagged with tape, which has been shown not to exclude aphids (J. M. Holland, pers. comm.). The aphids were enclosed in predator free smaller cages, which consisted of wire

Fig. 5. Schematic plan of the experimental area containing the beetle bank and enclosed and control areas positioned in the crop at four fixed distances away from the beetle bank

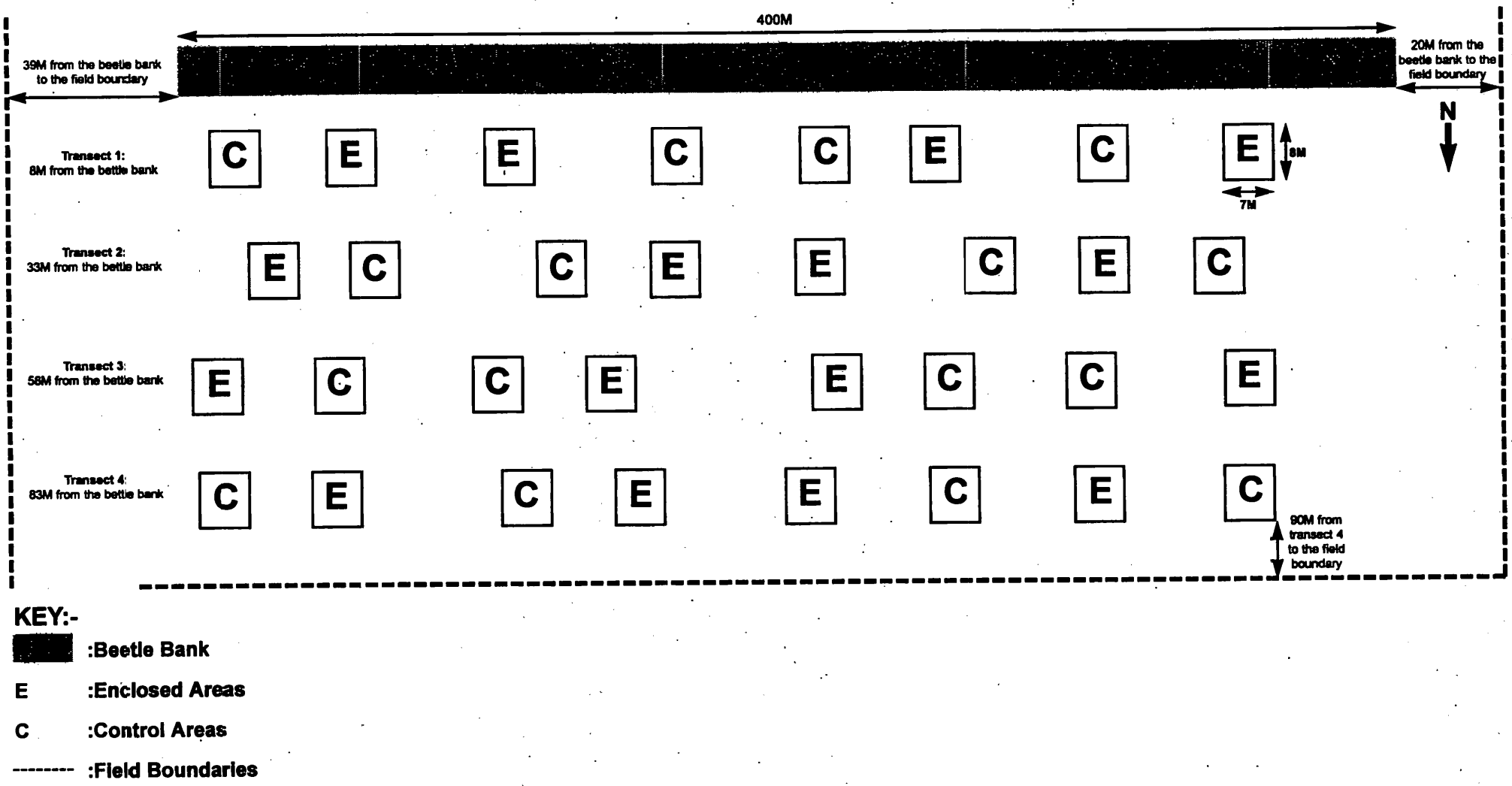


Plate 2. Creation of an enclosure using a tractor mounted barrier laying machine

Plate 3. Invertebrate sampling in an enclosure using a Dietrick suction sampler

frames covered in white mesh netting. The tops of the cages were covered with clear plastic when it rained to prevent aphid being knocked off the wheat plants.

On the 2 July the aphid cages were removed and aphid counting began. Alate and apterous *S. avenae* were counted on the twenty marked ears of wheat in each experimental area. As numbers were initially low, aphids were also counted on the wheat leaves. Recordings were taken twice a week until harvest.

Between the 25 July to the 19 August a further ten unmarked ears of wheat were randomly selected on one of the counting occasions each week, within each treatment and aphids were counted as for the twenty marked ears.

The numbers of predators and mummified aphids observed on the wheat ears and leaves were also recorded on each counting occasion.

The total mean number of aphids per tiller on the marked and unmarked tillers of wheat were $\log_e (x+1)$ transformed and analysed using repeated measures analysis of variance (ANOVA) with transect and treatment (enclosures vs. controls) as factors and date as the repeated measures factor (von Ende, 1993). Aphids recorded on the ears and leaves of the marked tillers of wheat were analysed separately. Significant interactions with date were explored using univariate ANOVA on each date separately. Where necessary means were investigated using Tukey's HSD test. The numbers of predators and mummified aphids observed on the wheat ears and leaves were also analysed as above.

A simple linear regression with groups was used to investigate whether the rate of population increase to the peak on the marked ears and leaves of wheat differed between the treatments (ie. enclosures and controls) and transects. These data were analysed using an accumulated ANOVA to explore the effects of treatment and transect, and the interaction between treatment and transect.

3.2.4 Monitoring of polyphagous predator composition within the enclosed and control areas

Three pitfall traps (8.5cm high and 6cm in diameter), with rain covers supported approximately 20cm above the top of the trap and containing ethylene glycol and detergent ("Fairy Liquid") to reduce the surface tension of the liquid, were placed at random within each treatment. Monitoring started on the 16 April 1996 and continued until the 31 July 1996. The traps were collected on a weekly basis and the invertebrates were preserved in alcohol before being identified at a later date in the laboratory.

Suction samples were also taken within the enclosed and control areas using a Dietrick suction sampler (D-vac) (Plate 3). Five sub-samples of ten seconds each ($0.46m^2$) were taken in each area. Monitoring commenced on the 25 April 1996 and continued until the 1 August 1996, with samples taken at 14 day intervals. The invertebrates sampled were frozen before being preserved in alcohol for identification at a later date.

All the samples were taken at least one metre away from the polythene barrier to avoid the effect of thigmotaxis, which is commonly observed in arthropods.

The total number of Carabidae, Staphylinidae, Araneae and all predators combined were $\log_e (x+1)$ transformed and analysed using repeated measures analysis of variance (ANOVA) with transect and treatment (enclosures vs. controls) as factors and date as the repeated measures factor (von Ende, 1993). Significant interactions with date were explored using univariate ANOVA on each date separately. Where necessary means were investigated using Tukey's HSD test.

Sub-groups within the above major taxonomic groups were also investigated, namely: 'highly ranked boundary carabids', 'boundary' type carabids, 'open-field' type carabids, '*Tachyporus* species', Linyphiidae and Lycosidae. Species belonging to the 'highly ranked boundary carabids', 'boundary' type carabids, 'open-field' type carabids and the '*Tachyporus* species' and the reasons why they are included in this thesis are described in Chapter 1 section 2.2. The Araneae were divided into Linyphiidae and Lycosidae as both these families have been found to be important in biological control but have different dispersal strategies. These four sub-groups were analysed as above. Numbers of individual

species were generally too low for analysis. However the total numbers of Aleocharinae, *Pterostichus melanarius*, *Bembidion* species, and *Trechus quadristriatus* were high enough in the pitfall traps to be analysed as above, though only the Aleocharinae and *Bembidion* species were abundant enough for analysis in the D-vac samples. During the study the family Cantharidae were also recorded in the D-vac samples and were therefore included in the analysis.

The relationship between the total number of each major taxonomic group at the aphid peak and the mean total number of aphids at the aphid peak was analysed using stepwise multiple regression. Data from the pitfall traps and the D-vac samples were analysed separately, and data were $\log_e (x+1)$ transformed.

3.3 RESULTS

3.3.1 Monitoring of *Sitobion avenae* numbers within the enclosed and control areas

The laboratory reared *S. avenae* released into the field did not establish well. Subsequent natural infestation occurred in early July.

There were no significant differences in the number of aphids on the leaves and ears of the marked tillers of wheat in the enclosed and control areas (Table 10 & Figs. 6 & 7). A significant interaction between transect and date was recorded for the marked leaves of wheat (Table 10). During the aphid peak, aphid numbers were greatest in the transects furthest from the beetle bank and lowest in those closest to the beetle bank, though not significantly. Univariate analysis on each date showed that aphid numbers only differed between transects on the 2 August ($F_{3,28} = 11.20$, $p<0.01$) and 6 August ($F_{3,28} = 3.82$, $p<0.02$) and aphid numbers were greatest in transect four on these dates (Fig. 8). As expected the number of aphids found on the ears and leaves of the marked tillers of wheat differed significantly with date as the aphid population increased and decreased. There were also no significant differences or interactions in the rate of population increase to the peak in the enclosed and control areas, or the transects on the marked tillers of wheat.

Fig. 6. Mean number of aphids per ear in the enclosures and controls on the marked tillers of wheat

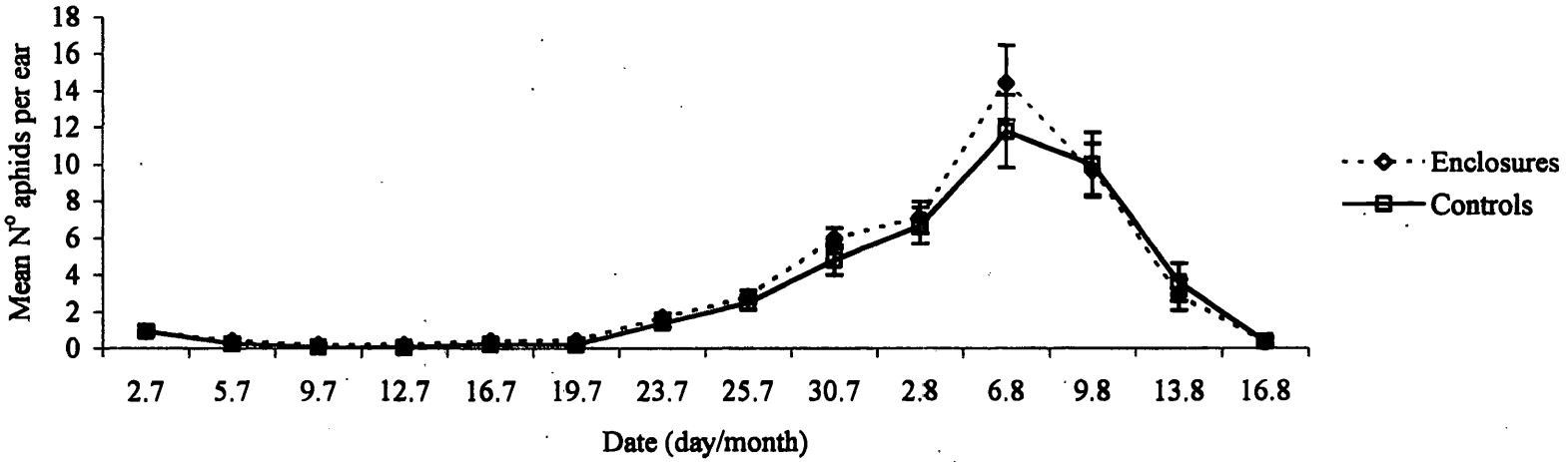
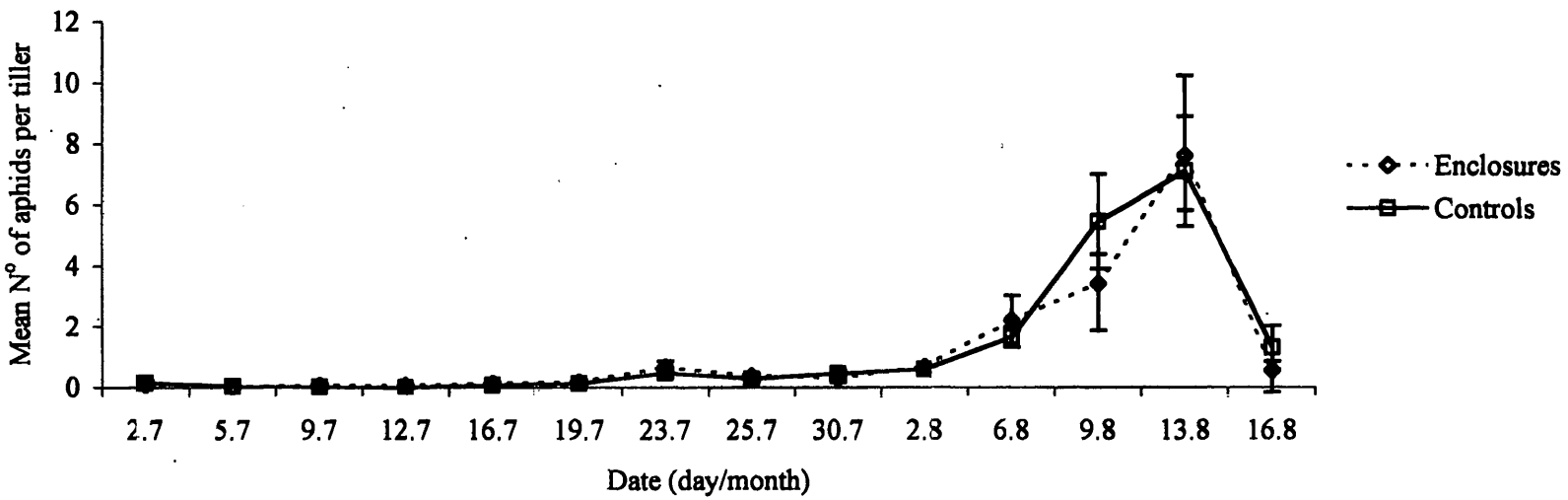


Fig. 7. Mean number of aphids per tiller in the enclosures and controls on the marked leaves of wheat



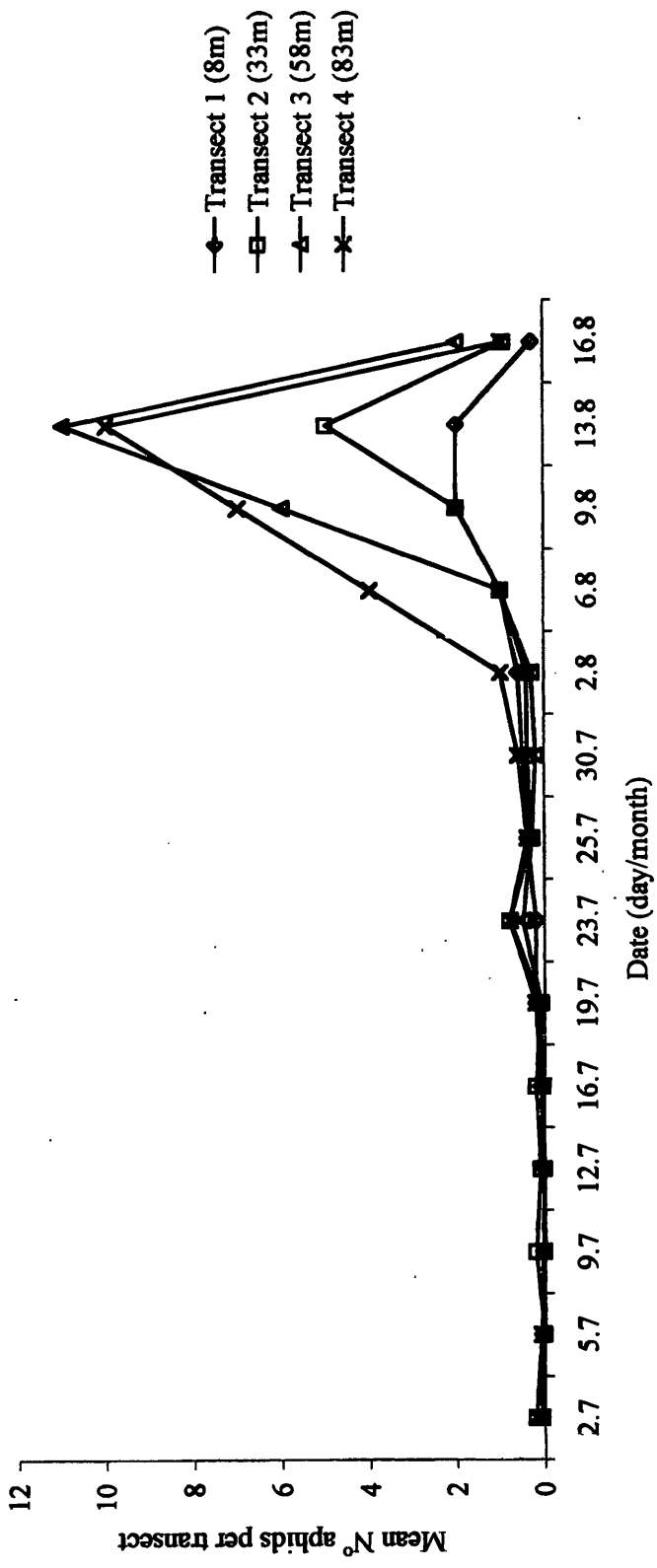


Fig. 8. Mean number of aphids per transect on the marked leaves of wheat

During the experiment it was noted that the marked tillers of wheat were becoming damaged due to over handling and did not appear to be ripening at the same rate as the rest of the crop. Consequently, a further ten ears of wheat were randomly selected on each counting occasion from the 25 July onwards. Analysis of the randomly selected (unmarked) ears of wheat showed a significant interaction between date and treatment with greater numbers of aphids in the enclosures compared to the controls (Table 10). At the peak of the infestation aphid numbers were 34% greater in the enclosures compared to the controls (6 August $F_{1,24} = 4.39$, $p<0.05$). Six days later when the aphid population was in decline numbers were still significantly (58%) greater in the enclosed areas ($F_{1,24} = 29.57$, $p<0.01$) (Fig. 9). A significant interaction between transect and date was also recorded for the unmarked ears of wheat (Table 10). Overall the number of aphids was lowest in transect one. Univariate analysis on separate dates showed that during the aphid peak numbers were significantly greater ($F_{3,24} = 3.12$, $p<0.04$) in transect four compared to transect one. Six days later in the aphid decline aphid numbers were still lowest in transect one compared to transects two and four ($F_{3,24} = 4.83$, $p<0.01$) (Fig. 10).

Table 10. Results of multivariate repeated measures ANOVA for aphids found on the marked tillers of wheat and the unmarked tillers of wheat, with date, transect and treatment (enclosures vs. controls) as factors (DF = degrees of freedom; F = variance ratio; P = probability level) (all data were $\log_e(x+1)$ transformed)

		Aphids on marked leaves		Aphids on marked ears			Aphids on unmarked ears	
Source	DF	F	P	F	P	DF	F	P
Treatment	1	0.16	0.69	2.05	0.16	1	9.27	0.01
Transect	3	2.39	0.09	0.39	0.76	3	3.31	0.04
Treatment x Transect	3	0.31	0.82	2.49	0.08	3	0.35	0.79
Date	13	42.03	0.01	134.48	0.01	4	240.81	0.01
Date x Treatment	13	0.62	0.84	0.60	0.86	4	5.23	0.01
Date x Transect	39	1.62	0.01	0.67	0.93	12	2.01	0.03
Date x Treatment x Transect	39	1.05	0.40	1.03	0.43	12	0.60	0.84

Fig. 9. Mean number of aphids per ear in the enclosures and controls on the unmarked ears of wheat

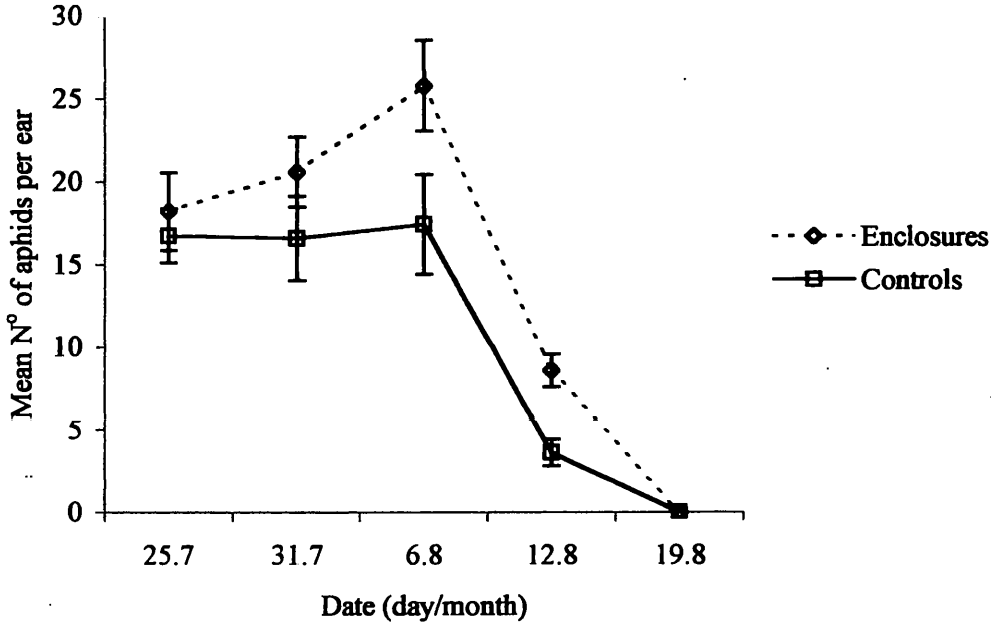
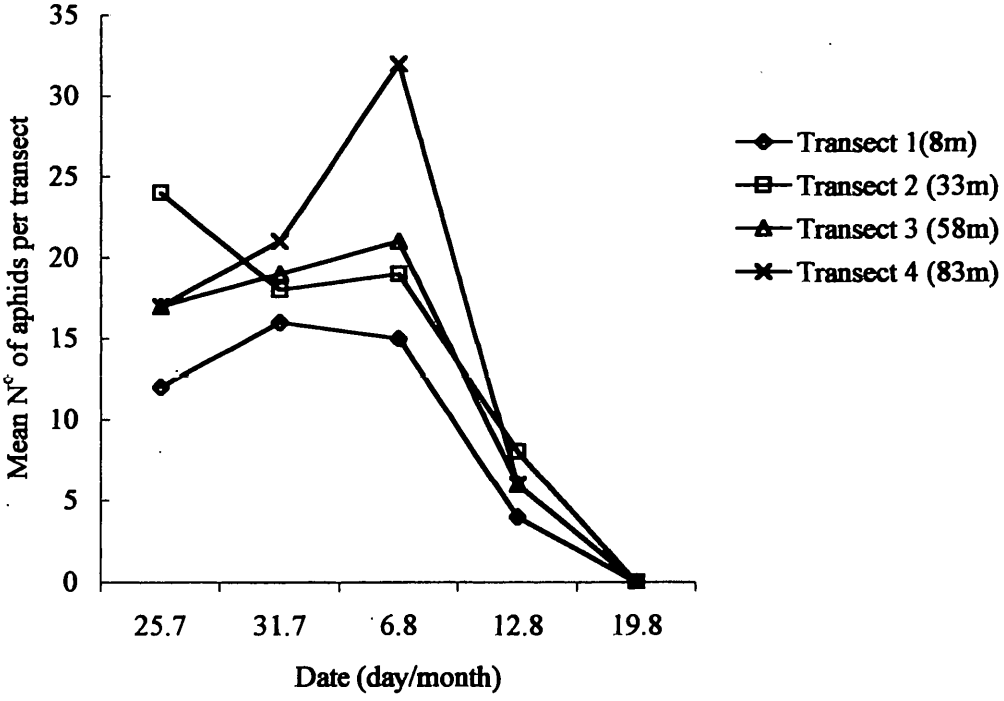


Fig. 10. Mean number of aphids per transect on the unmarked ears of wheat



The mean number (± one standard error) of aphids on the marked tillers and unmarked tillers of wheat in the enclosures and controls on each sampling date are given in Appendix VII.i-iii. The mean number (± one standard error) of aphids per transect on the marked leaves and unmarked ears of wheat on each sampling date are given in Appendix VII.iv-v.

There were no significant differences between the numbers of mummified aphids in the enclosed and control areas on either the marked or unmarked tillers of wheat. However the number of mummified aphids did differ significantly with date (marked ears $F_{13,312}$ = 17.98, $p<0.01$; marked leaves $F_{13,312} = 3.19$, $p<0.01$; unmarked ears $F_{4,96} = 17.68$, $p<0.01$) and there was a significant interaction between transect and date on the marked ears of wheat ($F_{39,312} = 1.65$, $p<0.01$). Mummified aphids did not start to appear until the aphid population was in the exponential increase phase and overall numbers were greatest in transects one and two. Even so the number of mummified aphids remained at relatively low levels peaking at 0.14 per tiller in early August.

The majority of predators observed on the tillers were aphid-specific Syrphidae and Chrysopidae larvae. Numbers of these predators recorded on the marked and unmarked tillers of wheat were low throughout the study (maximum of 0.03 per tiller in late July & August). Predators observed on the marked tillers of wheat only differed significantly with date (ears:$F_{13,312} = 2.50$, $p<0.01$; leaves: $F_{13,312} = 5.45$, $p<0.01$). Predators were recorded on the marked ears of wheat throughout the study with small peaks at the beginning of July and August. Predators observed on the marked leaves of wheat were most abundant during August.

Predators recorded on the unmarked tillers of wheat were significantly higher in the control compared to the enclosed areas ($F_{1,24} = 22.89$, $p<0.01$) and significantly greater in transect one compared to all the other transects ($F_{3,24} = 11.04$, $p<0.01$).

3.3.2 Monitoring of polyphagous predator composition within the enclosed and control areas

3.3.2.1 Pitfall trap data

The pitfall traps provided some indication of the activity/density of polyphagous predators found in the enclosed and control areas. Overall, the species caught in the traps were typical of those found on arable farmland.

All the predatory groups under investigation were significantly reduced in the enclosures compared to the controls. Overall the activity/density of the Carabidae was reduced by 37% in the enclosures compared to the controls. *Bembidion* species and 'highly ranked boundary carabids' were reduced by 72% and 67% respectively, and *Pterostichus melanarius* and *Trechus quadristriatus* by 17% and 35% respectively. The total number of 'boundary' type and 'open-field' type carabids were reduced by 56% and 31% in the enclosed areas respectively. The exclusion barriers were equally effective in reducing the Staphylinidae (by 46%) in the enclosed areas, including those species capable of flying eg. Aleocharinae 30% and *Tachyporus* 52%. However the exclusion barriers were least effective at excluding the Araneae (reduced by 24%). As expected the Lycosidae which are predominantly active on the soil surface were more efficiently reduced in the enclosures compared to the Linyphiidae which disperse aeronautically (57% and 24% respectively).

Several of the taxonomic groups under investigation showed a significant interaction between treatment and date, namely: the 'highly ranked boundary carabids', *Bembidion* species, *Pterostichus melanarius*, total Araneae and Lycosidae (Table 11). The 'highly ranked boundary carabids' were most active between April and June and during this time captures were greatest in the control areas, though only significantly so on the 5 June ($F_{1,30}$ = 8.18, $p<0.01$). The predominant carabid in this group was *Agonum dorsale*, closely followed by *Demetrias atricapillus*. *Bembidion* species were also more active between April and early June and were consistently reduced in the enclosures, but only significantly on 16 April ($F_{1,30}$ = 6.60, $p<0.02$), 30 April ($F_{1,30}$ = 8.08, $p<0.01$) and 5 June ($F_{1,30}$ = 5.62, $p<0.02$). Conversely *Pterostichus melanarius*, the second most abundant carabid after

Table 11. Results of multivariate repeated measures ANOVA of weekly pitfall trap catches for all predators combined and the major taxonomic groups, with date, transect and treatment (enclosures vs. controls) as factors (DF = degrees of freedom; F = variance ratio; P = probability level) (all data were $\log_e(x+1)$ transformed).

		Total polyphagous predators		Total Carabidae		Total Staphylinidae		Total Araneae		*Tachyporus* species		Aleocharinae		'Highly ranked boundary carabids'	
Source	DF	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Treatment	1	26.14	0.01	26.86	0.01	16.90	0.01	16.20	0.01	9.14	0.01	4.78	0.04	32.71	0.01
Transect	3	1.99	0.14	2.01	0.14	4.42	0.01	2.88	0.06	5.11	0.01	1.05	0.39	0.67	0.58
Treatment x Transect	14	0.62	0.61	1.22	0.33	0.13	0.94	0.05	0.99	0.30	0.83	0.44	0.99	0.25	0.86
Date	3	35.12	0.01	61.49	0.01	20.38	0.01	80.19	0.01	30.31	0.01	13.81	0.01	7.02	0.01
Date x Treatment	42	1.59	0.08	1.17	0.30	0.94	0.51	1.94	0.02	1.23	0.25	1.54	0.09	2.21	0.01
Date x Transect	14	1.89	0.01	1.95	0.01	1.39	0.06	0.91	0.63	1.90	0.01	1.10	0.32	1.49	0.03
Date x Treatment x Transect	42	0.67	0.94	0.86	0.72	0.65	0.95	1.24	0.15	0.54	0.99	0.79	0.83	1.20	0.19

Table 11. cont.

		'Boundary' type carabids		'Open-field' type carabids		*Bembidion* species		*Trechus quadristriatus*		*Pterostichus melanarius*		Linyphiidae		Lycosidae	
Source	DF	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Treatment	1	22.50	0.01	13.45	0.01	16.12	0.01	0.19	0.01	0.90	0.35	16.28	0.01	12.35	0.01
Transect	3	3.89	0.02	0.20	0.90	7.36	0.01	12.71	0.90	0.28	0.84	2.68	0.07	4.82	0.01
Treatment x Transect	14	0.72	0.55	0.69	0.57	0.34	0.80	0.52	0.67	0.93	0.44	0.03	0.99	0.14	0.94
Date	3	8.70	0.01	104.74	0.01	15.92	0.01	111.22	0.01	51.18	0.01	81.91	0.01	4.33	0.01
Date x Treatment	42	1.36	0.17	1.54	0.10	2.51	0.01	1.03	0.43	1.81	0.04	1.57	0.09	3.28	0.01
Date x Transect	14	1.70	0.01	1.86	0.01	1.89	0.01	2.29	0.01	1.34	0.08	0.96	0.55	1.44	0.04
Date x Treatment x Transect	42	0.94	0.58	0.85	0.73	1.05	0.39	0.67	0.94	1.09	0.33	1.26	0.14	1.06	0.38

Trechus quadristriatus, increased in abundance from July onwards within both the enclosed and control areas. Overall captures of *Pterostichus melanarius* were greater in the control areas though only significantly so at the beginning of the study (30 April $F_{1,30}$ = 24.77, $p<0.01$).

Araneae abundance was initially high at the beginning of the study in April but fell both in the enclosed and control areas during May and June before increasing again in both treatments from the end of June onwards. Overall Araneae abundance remained greatest within the control areas, significantly so around the time of the aphid peak (7 August $F_{1,30}$ = 5.88, $p<0.02$). The sub-group Lycosidae also showed a significant interaction between treatment and date. Lycosid abundance was greatest during April and early May, and was significantly greater in the controls compared to the enclosures (16 April $F_{1,30}$ = 7.46, $p<0.01$; 30 April $F_{1,30}$ = 9.55, $p<0.01$; 8 May $F_{1,30}$ = 4.68, $p<0.04$). Lycosid species found during the study included *Pardosa amentata*, *Trochosa ruricola* and *Pardosa prativaga*.

A significant interaction between transect and date was also recorded for several taxa namely: the total number of predators, total Carabidae, 'highly ranked boundary carabids', *Bembidion* species, 'boundary' type carabids, 'open-field' type carabids, *Trechus quadristriatus*, *Tachyporus* species and the Lycosidae (Table 11). A complex interaction between transect and date was found for total polyphagous predators with no easily identifiable pattern. However it appeared that total predator abundance was greatest in the transects closest (8m & 33m) to the beetle bank at the beginning of the study, after which predator abundance quickly increased in the transects furthest from the beetle bank (58m & 83m) exceeding that in the transects closest to the bank (8m & 33m). Towards the end of the study predator abundance fell in the transects furthest from the beetle bank and increased in the transects closest to the bank.

Although some emigration from the beetle bank into the crop appeared to be occurring for the Carabidae, the pattern was not clear. This was partly because the carabid group consisted of both 'boundary' type and 'open-field' type carabids, which showed different interactions between transect and date. Analysis of the 'boundary' type Carabidae indicated that a slow wave of emigration from the beetle bank into the crop was occurring. During April these carabids were significantly greater in the transects closest to the beetle bank (8m & 33m) compared to the transects furthest from the beetle bank (16 April: $F_{3,28}$ =

4.37, $p<0.01$; 30 April: $F_{3,28} = 4.14$, $p<0.02$) (Fig. 11). Between May and June 'boundary' type carabid abundance increased in the transects leading away from the beetle bank. By July 'boundary' type carabid abundance was more uniformly distributed across the field (Fig. 11). However during the first week of August, the abundance of 'boundary' type Carabidae appeared to be greatest in the transect closest to the beetle bank. A complex interaction between transect and date, with no easily identifiable pattern was found for the 'open-field' type Carabidae. The *Bembidion* group which was dominated by 'boundary' type carabids was also greatest in the transect (8m) closest to the beetle bank between April and May (Fig. 12). By June a more uniform distribution of this group was found across the field, though overall the activity/density of this group was greatest in the transects closest to the beetle bank (Fig. 12). Complex interactions between transect and date were also recorded for the 'highly ranked boundary carabids' and *Trechus quadristriatus*, with no easily identifiable patterns discernable.

The Staphylinidae were greatest overall in the transects furthest from the beetle bank (58m & 83m) as were the *Tachyporus* group throughout the study. The Lycosidae on the other hand showed a similar pattern of emigration from the beetle bank to the 'boundary' type Carabidae.

In the week prior (31 July) to the aphid infestation the total number of polyphagous predators ($F_{3,28} = 10.27$, $p<0.01$) and the total number of Carabidae ($F_{3,28} = 7.85$, $p<0.01$) were significantly greater in the transects closest to the beetle bank. During this time the 'open-field' Carabidae dominated the carabids, which were in turn dominated by *Trechus quadristriatus*. *Trechus quadristriatus* was also significantly higher in transects one and two compared to three and four immediately before the aphid peak ($F_{3,28} = 7.81$, $p<0.01$). Conversely in the weeks immediately prior to the peak of the aphid infestation *Tachyporus* species were greatest in the transects furthest from the beetle bank (3 July $F_{2,38} = 4.68$, $p<0.01$ & 24 July $F_{3,28} = 3.98$, $p<0.02$).

As expected all the taxonomic groups differed significantly with date and those mentioned above also showed significant interactions with date. This was because the experiment was conducted over a long period of time during which the phenology/activity of each taxon changed. Activity patterns of the 'highly ranked boundary carabids', *Pterostichus melanarius*, Bembidion species, total Araneae and Lycosidae are described above.

Fig. 11. Distribution of 'boundary' type Carabidae in the crop at varying distances from the beetle bank between late April and early August

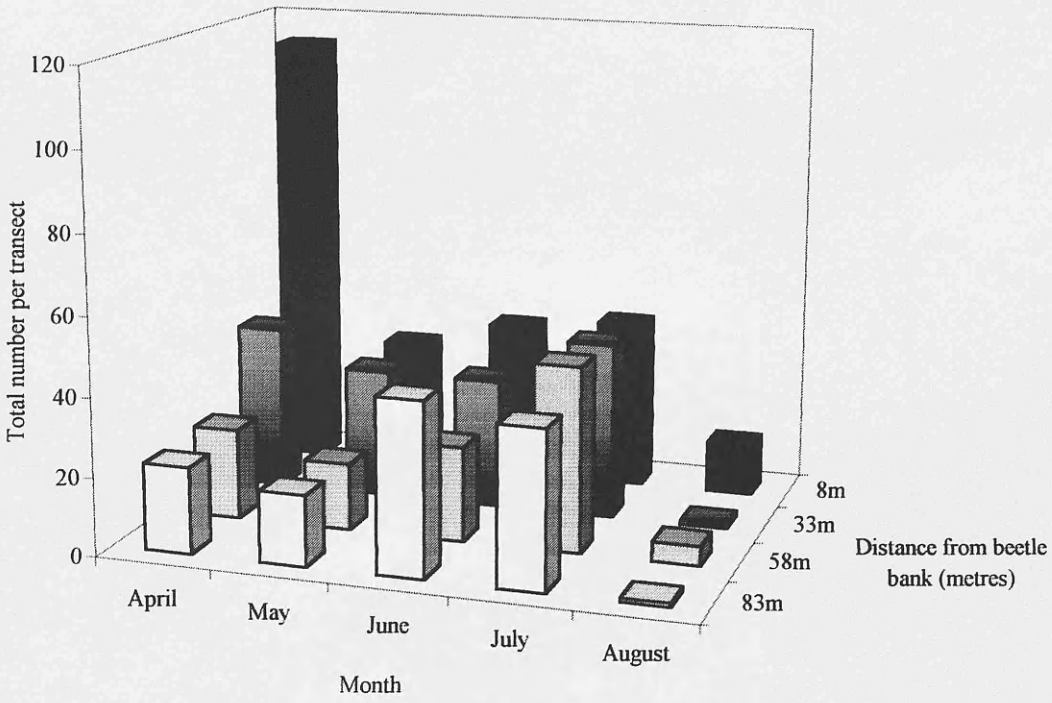
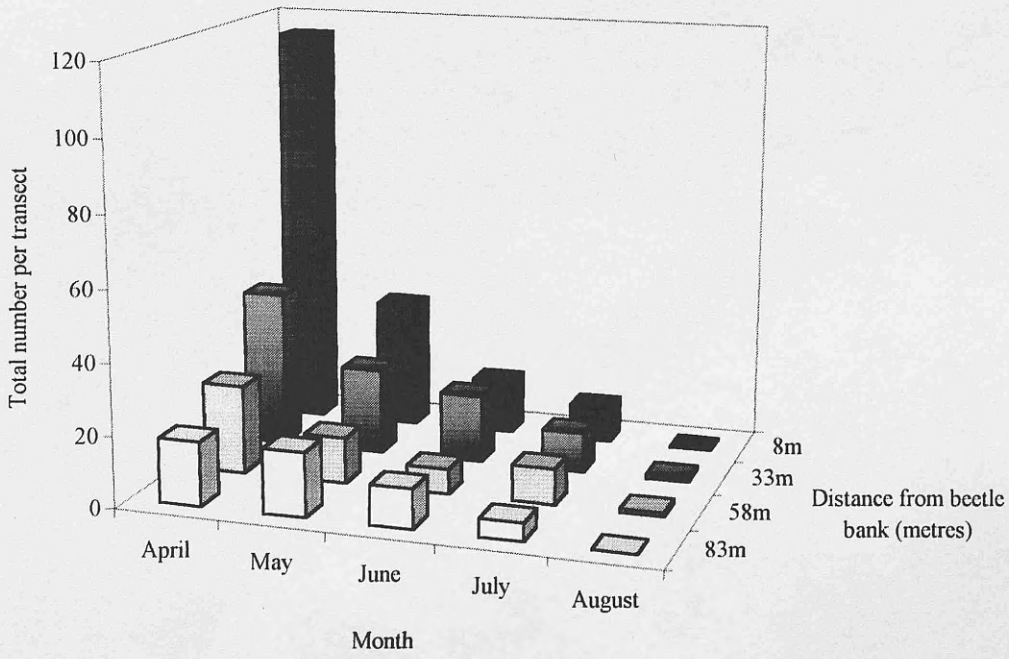
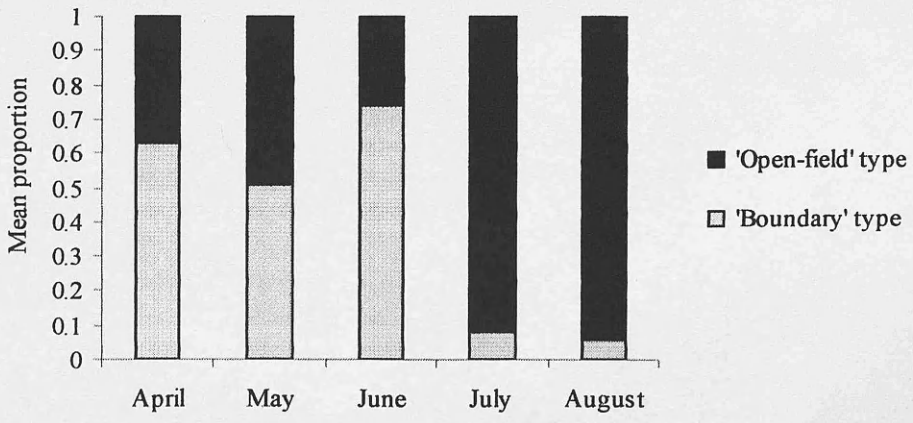


Fig. 12. Distribution of *Bembidion* species in the crop at varying distances from the beetle bank between late April and early August



The Staphylinidae were most abundant between May and early July as was the sub-group *Tachyporus* species. However the family Aleocharinae were more abundant later in the study from early June onwards. Total Carabidae were abundant throughout the study but were most abundant from mid June onwards. This reflects the increase in abundance of the two dominant carabid species *Trechus quadristriatus* which was most abundant later in the study around July and *Pterostichus melanarius* (described above). These two species are classified as being 'open-field' type carabids. Figure 13 indicates a pronounced change in the proportion of 'boundary' type carabids to 'open-field' type carabids between April and August. 'Boundary' type carabids were most abundant during April. Between April and May numbers of 'boundary' type carabids were marginally higher than those of 'open-field' type carabids. During June a small dip in 'open-field' type carabid abundance was recorded (Appendix VII. vi). However the abundance of 'open-field' type carabids increased greatly from July onwards, with numbers vastly exceeding those of the 'boundary' type carabids (Appendix VII. vi). Linyphiid abundance was greatest and continually increased on each counting occasion in both the enclosed and control areas in July. Other species known to prey on aphids such as the Cantharidae and aphid-specific Coccinellidae were rarely encountered.

Figure 13. The mean proportion of 'boundary' type and 'open-field' type carabids in the enclosed and control areas during each month of the study



The mean numbers (± one standard error) of each taxon caught in the pitfall traps in the enclosures and controls on each sampling date are given in Appendix VII.vi.

Stepwise multiple regression indicated that the total number of Araneae and Linyphiidae were significantly related to the mean total number of aphids on the unmarked ears of wheat at the aphid peak. 'Boundary' type Carabidae were significantly related to the mean total number of aphids on the marked ears of wheat at the aphid peak. The total number of Staphylinidae around the time of the aphid peak on the marked leaves of wheat (one week earlier) was significantly related to the mean total number of aphids on the marked leaves of wheat at the aphid peak (Table 12).

Table 12. Results of significant ($p<0.05$) stepwise multiple regressions comparing the total number of each taxon at the aphid peak in the pitfall traps with the mean total number of aphids at the aphid peak on the marked and unmarked tillers of wheat (all data were $\log_e (x+1)$ transformed).

Sampling method	Tillers marked/unmarked	Predatory group	r^2 value
Pitfalls	Marked ears	'Boundary' carabids	$r^2 = 0.37$, $y = -0.61 + 2.69x$
Pitfalls	Marked leaves	Staphylinidae	$r^2 = 0.11$, $y = -0.37 + 2.58x$
Pitfalls	Unmarked ears	Araneae	$r^2 = 0.24$, $y = -0.51 + 6.50x$
Pitfalls	Unmarked ears	Linyphiidae	$r^2 = 0.23$, $y = -0.51 + 6.43x$

3.3.2.2 D-vac sampling

Compared to the pitfall trap data, the D-vac samples underestimated the diversity and abundance of polyphagous predators found in the enclosed and control areas. This was partly because the D-vac technique is only suitable for small less mobile species which are day active. Therefore, many species typically found on arable farmland, such as *Pterostichus melanarius*, were not present in the samples.

Using this technique it was found that only *Tachyporus* species were significantly reduced (by 47%) in the enclosures compared to the controls (Table 13). Total Staphylinidae showed a significant interaction between treatment and date. Staphylinid abundance was greatest between April and early June in both the enclosed and control areas, and during

Table 13. Results of multivariate repeated measures ANOVA of weekly D-vac catches for all predators combined and the major taxonomic groups, with date, transect and treatment (enclosures vs. controls) as factors (DF = degrees of freedom; F = variance ratio; P = probability level) (all data were $\log_e$ (x+1) transformed).

		Total polyphagous predators		Total Carabidae		Total Staphylinidae		Total Araneae		*Tachyporus* species	
Source	DF	F	P	F	P	F	P	F	P	F	P
Treatment	1	0.12	0.73	0.09	0.35	2.18	0.15	1.57	0.22	10.45	0.01
Transect	3	0.85	0.48	0.61	0.61	1.98	0.14	1.56	0.22	1.87	0.16
Treatment x Transect	7	0.05	0.99	0.20	0.90	0.45	0.72	0.12	0.95	0.17	0.92
Date	3	38.31	0.01	5.90	0.01	59.49	0.01	3.74	0.01	21.56	0.01
Date x Treatment	21	1.93	0.07	1.80	0.09	2.75	0.01	1.19	0.31	1.59	0.14
Date x transect	7	1.14	0.31	1.79	0.02	0.73	0.80	0.84	0.66	0.76	0.76
Date x Treatment x Transect	21	0.79	0.72	0.45	0.98	1.08	0.37	0.90	0.59	0.75	0.78

Table 13. cont.

		Aleocharinae		'Highly ranked boundary carabids'		'Boundary' type carabids		'Open-field' type carabids		*Bembidion* species	
Source	DF	F	P	F	P	F	P	F	P	F	P
Treatment	1	0.09	0.77	0.24	0.63	0.46	0.50	0.63	0.43	2.42	0.13
Transect	3	1.42	0.26	1.34	0.28	1.63	0.21	0.03	0.99	3.78	0.02
Treatment x Transect	7	1.02	0.40	0.17	0.92	0.41	0.75	0.59	0.63	0.23	0.88
Date	3	41.62	0.01	5.96	0.01	3.73	0.01	5.53	0.01	7.18	0.01
Date x Treatment	21	1.93	0.07	1.30	0.25	1.07	0.39	1.50	0.17	1.08	0.38
Date x Transect	7	1.00	0.46	2.22	0.01	1.99	0.01	2.25	0.01	1.91	0.01
Date x Treatment x Transect	21	1.28	0.19	0.83	0.69	0.74	0.78	1.08	0.38	0.53	0.96

this time numbers were highest in the control areas. Few Staphylinidae were caught from mid June onwards, unlike the results from the pitfall trap data.

With the exception of the Araneae, Linyphiidae and 'highly ranked boundary carabids', all the other taxonomic groups were greater in the control areas, though not significantly so (Appendix VII.vii). The Araneae were dominated by Linyphiidae, with the exception of a few other species. No Lycosidae were captured by the D-vac.

The Carabid groups, namely: total Carabidae, 'highly ranked boundary carabids', 'boundary' type carabids, 'open-field' type carabids and *Bembidion* species, showed a significant interaction between transect and date (Table 13). No easily identifiable pattern could be distinguished for any of the taxa, particularly the 'open-field' carabids. However the total numbers of Carabidae, 'boundary' type Carabidae and the *Bembidion* species were greatest in transect one at the start of the study and increased in the transects furthest from the beetle bank over time, although *Bembidion* species abundance remained highest in transect one. Conversely the 'highly ranked boundary carabids' appeared to be greatest in transects three and four and lowest in transect one between April and early June.

As expected all the taxonomic groups varied with date. Total polyphagous predators were most abundant between April and late May/early June. A small peak in the middle of July was also observed. This pattern reflects the peak abundance of the three main taxonomic groups, namely the Carabidae and Staphylinidae, which were most active between late May and early June, and the Araneae which were most active in July. The sub-groups 'open-field' type carabids, 'boundary' type carabids, Aleocharinae, *Bembidion* species and *Tachyporus* species were abundant between April and early June, whereas the 'highly ranked boundary carabids' were most abundant from May onwards. Several species of Cantharidae were caught in the D-vac samples. Although some species have been shown to prey on aphids (Vickerman & Sunderland, 1975), their importance in the biological control of cereal aphids is unknown. Cantharidae did not start to appear in the crop until mid-June.

The results of the Carabidae and Staphylinidae caught by the D-vac do not mirror those results from the pitfall traps; reasons for these differences will be discussed in section 3.4.

The mean numbers (± one standard error) of each taxon caught in the D-vac samples in the enclosures and controls on each sampling date are given in Appendix VII.vii.

Stepwise multiple regression indicated that none of the taxa caught by the D-vac were significantly related to the mean total number of aphids on the marked or unmarked tillers of wheat.

3.4 DISCUSSION

3.4.1 The effect of polyphagous predators on aphid populations in the crop

The results from this experiment indicated that the 'enhanced' predator populations resulting from the beetle bank, did appear to have a significant impact on aphid populations in the crop. Significantly lower numbers of polyphagous predators in the enclosures compared to the controls, combined with significantly greater numbers of aphids in the enclosures, strongly suggests that polyphagous predation was responsible for reducing aphid numbers. Aphid populations were significantly lower in the transects closest to the beetle bank compared to those furthest from the bank, indicating that polyphagous predation was greatest closest to the beetle bank.

The marked tillers of wheat suffered noticeably from repeated handling and so may not have given a result typical of the field as indicated by the unmarked tillers. Also, polythene bags were placed over the top of the wire cages containing the introduced aphids, to prevent them being washed off by the rain whilst they were establishing. This may have altered the micro-climate of the wire cages, as ripening of the marked ears was delayed. Therefore, the marked ears (and possibly leaves) were probably not representative of the population of wheat ears as a whole.

The late infestation and rapid build up of the natural aphid population probably outstripped predation by polyphagous predators, resulting in an aphid outbreak. Previous studies have shown that polyphagous predators exert the greatest effect on aphid population development when aphid populations build up slowly, during the spring and early summer

(Edwards *et al.*, 1979; Chiverton, 1986 & 1987; Burn, 1992). Theoretically this is when predator to prey ratios are high and the potential for aphid control is optimal (Chiverton, 1987). Several studies have shown that only a few species of polyphagous predator such as *Tachyporus hypnorum* and *Agonum dorsale* are active early enough during spring and early summer to inhibit aphid population development (Edwards *et al.*, 1979; Coombes & Sotherton, 1986; Chiverton, 1987; Sunderland *et al.*, 1987a). Sunderland & Vickerman (1980), and Sunderland *et al.* (1986) also gave these predators a high ranking in terms of their importance as cereal aphid predators, as they exhibited high predation indices on cereal aphids during the aphid establishment phase.

In this experiment aphids were not observed during the period when these 'highly ranked predators' were abundant (April-June). The highly ranked predators in this study included the 'highly ranked boundary carabids' and *Tachyporus* species which have also been observed overwintering on beetle banks (Thomas *et al.*, 1991 & 1992a; McLeod, 1994; Collins *et al.*, 1996). *Tachyporus* species dominated the Staphylinidae which were negatively related to the number of aphids at the aphid population peak, thus indicating the potential importance of this family, in particular *Tachyporus* species, in controlling aphid populations. Dennis and Wratten (1991) provided further evidence for the importance of *Tachyporus* species in the biological control of cereal aphids. Using cages to exclude all but the staphylinid species under investigation, these researchers showed that *Tachyporus obtusus* and *Tachyporus chrysomelinus* could reduce numbers of *Sitobion avenae* prior to the exponential phase of aphid population increase. The group 'boundary' type carabids which includes many aphid eating species, such as those in the group 'highly ranked boundary carabids', was also negatively related to the number of aphids at the aphid population peak. Other predators, which were more abundant in April and early June before the onset of the aphid invasion included, the Lycosidae and *Bembidion* species. Many of the species that comprised the Lycosidae and *Bembidion* in this experiment, have been recorded overwintering on beetle banks and have been shown to prey on cereal aphids. For example, *Bembidion lampros* and *Pardosa amentata* (Sunderland & Vickerman, 1980; Chiverton, 1987; Sunderland *et al.*, 1987a; Nyfeller & Benz, 1988; Thomas, 1991; Chapter 2).

Only the Aleocharinae, Linyphiidae and total Carabidae were abundant around the time of the aphid invasion. The Carabidae during this period were dominated by 'open-field' type

species that are most active during mid-late summer, such as *Pterostichus melanarius* (Edwards *et al.*, 1979). Experimental evidence has shown that species belonging to these taxa generally appear too late to exert any control on aphid population growth, as aphid populations are usually already in the exponential phase by mid-late summer (Edwards *et al.*, 1979; Chiverton, 1987). Aleocharinae species have been found not to react positively to an ELISA test with cereal aphid antiserum (Sunderland & Vickerman, 1980), but Sunderland *et al.* (1987a) suggested they should not be dismissed as cereal aphid predators. Aleocharinae were abundant during the summer in this experiment and have also been found overwintering on beetle banks (Chapter 2). Therefore the Aleocharinae deserve further investigation, although as mentioned above their appearance later in the summer may mean they would have less of an impact on aphid populations, compared to predators active in spring and early summer.

During the summer the two dominant Carabidae were *Pterostichus melanarius* and *Trechus quadristriatus*. These two species spend their entire life cycle in cereal crops/open-fields (Sotherton, 1984). They have also been shown to prey on cereal aphids (Sunderland & Vickerman, 1980; Chiverton, 1987; Sunderland *et al.*, 1987a; Holland *et al.*, 1996), although the main prey of *Pterostichus melanarius* is thought to be other adult Coleoptera (Sunderland, 1975). *Pterostichus melanarius* and *Trechus quadristriatus* were abundant in high numbers at the time of the aphid infestation and may have been responsible for the reduction in aphid densities in the controls compared to the enclosures. However the potential of these species in controlling aphid populations may have been underestimated because of the climatic conditions which persisted at the time. During the aphid infestation the weather was particularly warm and dry and this may have reduced predation rates because beetles were sheltering during the day to prevent desiccation (Holland *et al.*, 1996). Although numbers of *Pterostichus melanarius* were significantly reduced in the enclosures, the difference between the enclosures and controls was not as great as expected. *Pterostichus melanarius* caught in the enclosures may have consumed a larger proportion of aphids because some of their alternative prey may have been excluded or trapped out (Holland *et al.*, 1996). Therefore the effect of reducing polyphagous predation by the exclusion barriers may have been underestimated in this experiment. However this would have to be confirmed by gut dissections or ELISA.

The Linyphiidae may also have played a role in reducing overall aphid numbers in the control areas, where they were found in significantly higher numbers compared to the enclosed areas. Many linyphiids have been shown to prey on aphids (Sunderland *et al.*, 1987a), several of which were present in this experiment, and have also been found on beetle banks during the winter. For example, *Erigone atra* and *Lepthyphantes tenuis* (Sunderland *et al.*, 1987a; Chapter 2). The results from this study and others like it (Chiverton, 1986; Holland & Thomas, 1997a) indicated that there is a negative relationship between the Araneae, in particular the Linyphiidae, and the number of aphids at the aphid population peak. This highlights the potential importance of this family in the control of cereal aphid populations. Linyphiidae also contribute to the biological control of cereal aphids in a rather different way. Sunderland *et al.* (1986) found that linyphiid webs can cover more than 50 % of a field by late July, and they showed that small aphids falling into these webs are unlikely to escape, even if the spider is satiated or absent. Furthermore linyphiids are well adapted by means of their dispersal, reproductive and feeding strategies, to utilise ephemeral habitats such as cereal fields (Ford, 1977; Anderson, 1974; Maelfait & De Keer, 1990; Duffey, 1993; Halley *et al.*, 1996; Topping & Sunderland, 1998). Therefore this family is potentially one of the most important predatory groups in cereal crops.

The micro-climate effect created by the enclosures cannot be dismissed as a probable cause of the difference recorded in aphid numbers between the enclosures and controls. Wind and rain have been shown to dislodge aphids from wheat plants (Mann *et al.*, 1995) making them available to ground predators (Winder *et al.*, 1994). Reduced wind speeds caused by the plastic barriers may have contributed to fewer aphids falling to the ground to be eaten by soil surface inhabiting predators caught in the enclosed areas. However, the height of the barrier was low in relation to the height of the wheat ears and the enclosures were large, so the effect was unlikely to be great. Randomly selecting wheat plants 1m away from the plastic barriers also aimed to overcome this problem. The enclosures may also have affected the abiotic environment for the predators. For example, relative humidity and ground temperatures may have been higher in the enclosures compared to the controls. Higher temperatures in the enclosures could have increased predator activity and consequently increased predator-prey encounter and predator consumption rates, resulting in increased predation pressure (Scheller, 1984; Sopp & Wratten, 1986; Chiverton, 1988; Lang *et al.*, 1999). Therefore yet again the effect of reducing polyphagous predation by

the exclusion barriers may have been underestimated. Further studies are needed to investigate whether there are any significant differences in the abiotic environment between enclosed and control areas.

Despite numerous experiments documenting the importance of polyphagous predators in preventing aphid population growth (Edwards *et al.*, 1979; Sunderland & Vickerman, 1980; Chiverton 1986 & 1987; Sunderland *et al.*, 1987a; Ekbom *et al.*, 1992), several other experiments have indicated that many 'highly ranked cereal aphid predators', prefer alternative prey to cereal aphids. For example, *Erigone atra* and *Agonum dorsale* (Toft, 1995; Bilde & Toft, 1994; Bilde & Toft, 1997). However results from these feeding experiments, are often difficult to interpret as they are performed under laboratory conditions, which do not represent real field conditions. The disparity between field and laboratory evidence, maybe explained by the availability of preferred prey and the hunger level of predators in different seasons in the field. Food scarcity is probably a commonly occurring situation in the field (Juliano, 1986; Van Dijk, 1986; Bommarco, 1998), with prey availability governed by multitude of factors. Bommarco (1998) suggested prey availability maybe influenced by the spatial complexity of the agricultural landscape. A reduction in plant diversity in landscapes dominated by monocultures may result in lower prey abundance and diversity compared that in more heterogeneous landscapes (Lawton, 1978; Bommarco, 1998). Bilde and Toft (1997) found that the hunger level of *Agonum dorsale* was higher during the aphid establishment phase in spring, decreasing to lower levels in mid-summer. If alternative prey are in short supply during this period and predators are forced to survive on a diet of less preferred prey (ie. aphids), then this may explain why these species are such good aphid predators. These findings may also explain why polyphagous predators are unable to control aphids once the exponential phase has started. Neither functional nor numerical responses to aphid aggregations are likely to be significant in species with low preference for aphids (Toft, 1995). However there is some evidence to contradict this theory, which is discussed below. If there is a trend towards polyphagous predators having a low preference towards aphids, then a general increase in the population of predators would increase the efficiency in aphid predation (Sunderland *et al.*, 1986; Alderweireldt, 1994a & 1994b; Bilde & Toft, 1997). Beetle banks may therefore be important in enhancing predator populations if maximum predation of cereal aphids is to be achieved.

Recent research has found a synergistic interaction between foliar-foraging and ground-foraging predators and their ability to suppress aphid populations, which may also be influenced by prey density (Losey & Denno, 1998). Losey and Denno (1998) showed that the combined predation rate of both foliar (*Coccinella septempunctata*) and ground (*Harpalus pennsylvanicus*) foraging predators on the pea aphid (*Acyrthosiphon pisum*) was significantly greater than the sum of their individual predation rates in laboratory experiments. However this interaction was only significant at high prey densities. Field experiments also showed that the combined impact of these two predators on aphid population growth was significantly greater than the sum of their individual impacts. The mechanism behind this interaction was the 'dropping' response elicited by *Coccinella septempunctata*, which rendered the aphids susceptible to predation by *Harpalus pennsylvanicus* on the ground. If similar responses by aphids are elicited by climbing predators abundant early in spring (eg. *Tachyporus hypnorum*) when aphid populations are low then this interaction could be vital in destabilising aphid populations whilst they are still in the establishment phase. Losey and Denno (1998) concluded that factors that disrupt the synchrony of predator guilds, could deter this synergistic interaction. For example many ground-foraging predators disperse from overwintering sites in the spring by walking. Therefore in large cereal fields these predators may still be in close association with field boundaries during the aphid establishment phase (Coombes & Sotherton, 1986). Conversely many foliar-foraging predators disperse by flying and will have already fully colonised the crop during this period (Coombes & Sotherton, 1986). If predator-predator interactions occur with 'highly ranked cereal aphid predators' which are active in early spring and which disperse by flying and walking, then this disruption could potentially lead to increases in aphid population growth, particularly in field centres where aphid populations are generally higher (Chambers *et al.*, 1982; Coombes & Sotherton, 1986). Beetle banks reduce field size and aim to enable predators that disperse by walking to fully colonise crops before the onset of an aphid invasion. Therefore beetle banks may also be important in optimising the impact of these synergistic interactions.

Although preliminary work by Thomas *et al.* (1991) indicated that a wave of predator emigration did occur away from beetle banks, recommendations on the spacing of beetle banks in cereal fields to optimise the dispersal of predators (particularly those that disperse by walking) are vague. Unfortunately the results from this experiment did not provide conclusive evidence on how far predators penetrate into the crop from beetle banks, or

how the banks affect the phenology of dispersal of these predators, in terms of the timing of movement in relation to aphid population increase. A slow wave of dispersal away from the beetle bank did appear to occur for the 'boundary' type Carabidae. However, these carabids were generally more abundant in the transects closest to the beetle bank between April and early June when the ratio of predator to aphid numbers is usually high and the potential to prevent an aphid outbreak is greatest. A similar pattern appeared to occur with the *Bembidion* species and Lycosidae though this was not as clear as it was for the 'boundary' type carabids. Thomas *et al.* (1991) described a wave of emigration away from a beetle bank by *Demetrias atricapillus* and *Tachyporus hypnorum* during the spring. However no such wave was found in this experiment for either the group *Tachyporus* or 'the highly ranked boundary carabids' to which *Demetrias atricapillus* belonged. Similar results were reported by Coombes and Sotherton (1986), who found no wave of dispersal by *Tachyporus* species away from field boundaries during the spring. *Tachyporus* species disperse by flying and can cover greater distances in a shorter space of time compared to many carabids, resulting in more rapid colonisation of cereal crops (Coombes & Sotherton, 1986). The true impact of the beetle bank on predator dispersal is also difficult to distinguish because predators may have been dispersing from nearby field boundaries into the experimental area, therefore making the effects of the beetle bank harder to determine.

Significantly lower aphid populations in the transects closest to the beetle bank compared to those furthest from the bank indicated that predation was greatest close to the beetle bank. Thomas (1989) also investigated the effect of early season predation of artificial prey items by predators emigrating from a beetle bank. He found that the predation was greatest on the beetle bank itself and in its immediate environment. These results may indicate that the majority of predators do not migrate very far from beetle banks. One explanation for this maybe that beetle banks provide an alternative source of prey for predators other than the crop. Although evidence to discount this theory is lacking, competition for prey on beetle banks would probably force predators into the crop in search of alternative prey although, as mentioned above how far these predators would emigrate is unknown. Experiments investigating the effect of weedy strips on the dispersal of predators in cereal crops have also found that predators do not migrate very far into crops from the strips (Lys & Nentwig, 1992; Frank, 1997). The effect of beetle banks on the dispersal and phenology of dispersal of predators into the crop is further investigated in Chapter 4.

This study also indicated that the beetle bank could have influenced the distribution of aphid-specific predators in the crop. The number of predators (mainly aphid-specific larvae) and mummified aphids observed on the wheat ears were significantly greater in the transects closest to the beetle bank. The beetle bank may provide a nectar resource for adult Syrphids during the summer and an overwintering site for adult Chrysopidae during the winter. However the numbers of aphid-specific predators and mummified aphids were low and were unlikely to have had a significant effect on the aphid population (Chambers *et al.*, 1986). The number of adult aphid-specific predators could be enhanced in cereal fields during the summer by providing adequate nectar resources on beetle banks. No Chrysopidae were found overwintering on beetle banks in experiments detailed in this thesis. However commercially available overwintering 'boxes' are also now available for Chrysopidae, which could be placed on beetle banks and in field margins to encourage these invertebrates on farmland.

3.4.2 Efficiency of the enclosures in excluding polyphagous predators and the techniques used to sample different predatory groups

The results from the pitfall trap catches indicated that all the taxa under investigation were significantly reduced in the enclosures compared to the controls. However the exclusion barriers in this experiment appeared to be less efficient at reducing Carabidae and Linyphiidae in the enclosed areas than those used in other studies (Edwards *et al.*, 1979; Chiverton, 1987; Holland, 1998). This was probably related to the different number and type of pitfall traps used in this study, and problems encountered with maintaining the polythene barriers and pitfall traps during the summer.

The summer of 1996 was particularly warm and dry, causing the clay soil in the field to crack, often creating deep fissures. Cracking and shrinkage of the soil around the pitfall traps occurred on several occasions, reducing the efficiency of this sampling technique. The dry weather may also have affected the efficiency of the exclusion barriers. Although the plastic barriers were buried approximately 15cm into the ground, it is possible that some of the fissures in the soil were deep enough around the sides of the enclosure to allow predators to burrow underneath the barriers. This may have been the case for *Pterostichus melanarius*. Although *Pterostichus melanarius* was significantly reduced in the enclosures compared to the controls, the difference was not as great as expected. This

carabid overwinters in the crop and would have been trapped in the enclosures as the adults emerged from the soil. This is also the case for *Trechus quadristriatus*, however this carabid was more effectively reduced in the enclosures (35%) compared to *Pterostichus melanarius* (17%). As the summer progressed and the population of *Pterostichus melanarius* increased, numbers both in the enclosed and control areas increased and the difference between the two treatments diminished. Increasing the number of pitfalls in each treatment might have partly overcome this problem. At the end of the study large numbers of dead *Pterostichus melanarius* were found in the lining of the plastic barriers. Luff (1986) showed that some carabid beetles aggregate in pitfall traps, probably in response to aggregation or sex pheromones or defensive secretions. It is possible that a similar effect was happening with the enclosures and the beetles attracted to these dead and dying carabids were gaining access into the enclosures because of the cracks in the dry soil surrounding the barriers. There may however have been a similar amount of emigration from the enclosures, which would have counteracted this.

It is not surprising that the Linyphiidae were not as effectively reduced by the exclusion barriers as the other taxa. This family disperses mainly by ballooning and could therefore easily enter the enclosures. Topping and Sunderland (1992) have also shown that pitfall traps are less efficient at capturing linyphiids than carabids. In this study linyphiids were often observed making webs above the traps. However the Linyphiidae were significantly reduced in the enclosed areas and the plastic barriers may have had some effect, possibly visual, in deterring this family, though it is difficult to distinguish between the effects of the barriers and those of the pitfall traps on the observed reductions (Holland, 1998). Surprisingly the Staphylinidae were more effectively reduced in the enclosures than the Carabidae and Linyphiidae, with reductions similar to those reported by other studies (Holland, 1998). Although some staphylinids disperse by walking many disperse by flying and again the barriers may have had some visual deterrent.

Pitfall traps vary in their effectiveness for capturing different species of predator depending on the material they are made of, the shape and size of the trap, and the preservative used in the trap (Luff, 1975; Holopainen, 1990). Further criticisms of this method of sampling are discussed in Chapter 4. As mentioned above Topping and Sunderland (1992) found that pitfall trapping was less effective for capturing linyphiids compared to carabids. Pitfall traps are also less efficient at capturing small carabids

compared to larger carabids (Hassall and Wratten, 1988). Large carabids are generally faster moving and cover greater distances than smaller carabids and are therefore more likely to encounter traps (Greenslade, 1964). Smaller carabids are also more likely to avoid capture by the traps because they can recover their balance, if unbalanced, upon coming across a trap lid (Hassall and Wratten, 1988). *Demetrias atricapillus* a small commonly occurring carabid on farmland is poorly represented in pitfall traps because the adhesive setae on the tarsi of this species make it an adept climber enabling it to avoid capture by traps (Lindroth, 1974; Stork, 1980; Hassall & Wratten, 1988). *Demetrias atricapillus* was included in the group 'highly ranked boundary carabids', an important group in this study. Linyphiid and small carabids may have been under sampled using this method in this study.

Suction samples are commonly used to sample smaller lightweight carabids and spiders (McLeod *et al.*, 1995; Stewart & Wright, 1995; Sunderland *et al.*, 1995). However the results from the D-vac suction samples in this study indicated that this technique was less efficient at sampling some of the smaller species of carabid and vastly underestimated the abundance of Araneae/Linyphiidae compared to the pitfall trap results. MacLeod *et al.* (1995) also reported that the densities of predators on arable farmland can be underestimated using large suction samplers similar to the D-vac. It can therefore be concluded that the abundance and activity/density of many of these species was underestimated by both sampling methods in this experiment. D-vac efficiency can vary in accordance to height of vegetation and environmental conditions (ie. moisture on vegetation) (Sunderland *et al.*, 1995). Because D-vac samples only sample at one point in time, unlike pitfall traps, weather variability which affects predator activity (Briggs, 1961) is more likely to bias suction sample results. Nocturnal species will also be under-represented in samples taken during the day, particularly as a large number of nocturnal species are found below ground during the daytime (Luff, 1978; Kegel, 1990). During the hot dry weather many predators may also have been missed by the vacuum sampler because they were sheltering in the deep soil fissures and were therefore below the level of influence of the D-vac. Lycosidae were not caught in the D-vac samples in this study, despite their light weight. D-vacs make a considerable amount of noise and vibrations, which may alert highly mobile predators such as the Lycosidae to the oncoming sampler, therefore allowing them to escape by fleeing the area. The efficiency of the D-vac technique could be enhanced by using one of the newer versions of suction sampler that

are being promoted (Stewart & Wright, 1995; MacLeod *et al.*, 1995). The smaller aperture for collecting predators on the newer devices increases air velocity which aids the capture of predators (Stewart & Wright, 1995; MacLeod *et al.*, 1995). However the smaller aperture is likely to be a hindrance when sampling tall crops and the efficiency of sampling taller vegetation with this kind of device may be reduced. The narrow aperture may also be susceptible to errors caused by 'edge effect' compared to machines with larger apertures (MacLeod *et al.* 1995). The efficiency of this sampling technique will also be discussed further in Chapter 4.

The pitfall traps in this experiment could only provide an estimate of the activity/density of predators. Carabid activity is thought to be governed by a number of factors including hunger (Mols, 1979). The availability of food, may have differed across the field and in the enclosed and control areas, thereby affecting the results. Gut dissections of the predators caught in the experiment would have provided some evidence to confirm this. Other techniques such as fenced pitfall traps and ground photo-elector traps (Sunderland *et al.*, 1995) would provide a better estimate of predator density, enabling more thorough interpretation of results. Sunderland *et al.* (1987b) combined pitfall trapping and vacuum net sampling with ground surface searching, to attempt to obtain an accurate estimation of invertebrate density in cereals. They concluded that a combination of sampling methods provided a more accurate estimate of predator density compared to single sampling techniques. However this combined approach is time consuming and labour intensive, particularly if the surface searching method is considered (Sunderland *et al.*, 1987b; Sunderland *et al.*, 1995). This method of sampling was not feasible in this experiment due to time constraints.

3.5 SUMMARY

This experiment indicated that polyphagous predators emigrating from beetle banks can significantly reduced aphid populations in the crop. However several questions still remain unanswered. Firstly, it is still not known what field density of predators is required to prevent economic loss by cereal aphids (Holland & Thomas, 1997b). As suggested by Holland and Thomas (1997b) the use of area dependant sampling techniques, for example the fenced pitfall trap (Sunderland *et al.*, 1995), would help identify densities where

polyphagous predators are having an impact. Secondly, further experiments are needed to investigate the impact of polyphagous predators emigrating from beetle banks on aphid populations, in years when aphid populations build up slowly during spring and early summer. Finally, it is still not known exactly how far predators emigrate into the crop from beetle banks and how the timing of dispersal is related to aphid population increase in the crop. Until this question is answered, recommendations on the optimal spacing of beetle banks in fields in order to maximise predator dispersal cannot be made. The impact of beetle banks on predator dispersal in crops is examined further in Chapter 4.

CHAPTER 4.

THE IMPACT OF BEETLE BANKS ON THE DISPERSAL AND DISTRIBUTION OF POLYPHAGOUS PREDATORS IN CEREAL CROPS

4.1 INTRODUCTION

It has been well documented that many polyphagous predators that are important in the biological control of cereal aphids overwinter almost exclusively in field boundary habitats (Sunderland & Vickerman, 1980; Sotherton, 1984 & 1985; Andersen, 1997). Many of these predators, in particular the carabids, disperse slowly into the crop from boundary habitats during spring by walking (Coombes & Sotherton, 1986). Aphid populations are often distributed non-randomly in cereal crops and are higher in the middle of fields during May/June than at field edges (Chambers *et al.*, 1982; Coombes & Sotherton, 1986). In large cereal fields, predators that disperse by walking may still be in close association with field boundaries at a time when aphid populations are increasing slowly (Coombes & Sotherton, 1986). Therefore aphid populations may grow unchecked in the absence of sufficient polyphagous predation in the centre of large cereal fields.

Beetle banks aim to reduce the size of large fields by creating an overwintering resource for polyphagous predators in the centre of cereal fields (Thomas *et al.*, 1991). By enhancing predator numbers in the centre of cereal fields and reducing field size, it has been hypothesised that predators, especially those that disperse by walking, will be able to fully colonise a cereal crop before the onset or in the early stages of an aphid invasion (Thomas *et al.*, 1991). However there is little evidence to support this theory and an experiment detailed in Chapter 3 of this thesis, indicated that some predatory groups may remain in close association with beetle banks, rather than fully colonising the crop during the spring and summer. A final experiment was therefore conducted to further investigate the effectiveness of beetle banks in promoting predator dispersal throughout cereal crops. This was performed by recording the effect of the presence or absence of a beetle bank in cereal fields on polyphagous predator distribution in the crop during spring and summer.

4.2 MATERIALS AND METHODS

4.2.1 Study sites

Ten fields were selected for the study, five containing beetle banks and five without beetle banks. Since it was difficult to find ten fields all of exactly the same size, fields with and without beetle banks were paired according to field size and crop type (ie. five pairs of fields existed each containing a field with and without a beetle bank). Two crop types were used in the study: winter wheat and winter barley. In the fields containing beetle banks the same crop type was sown on either side of the beetle bank with the exception of the fields containing the beetle banks in pairs 1, 2 & 3 (Appendix VIII.i).

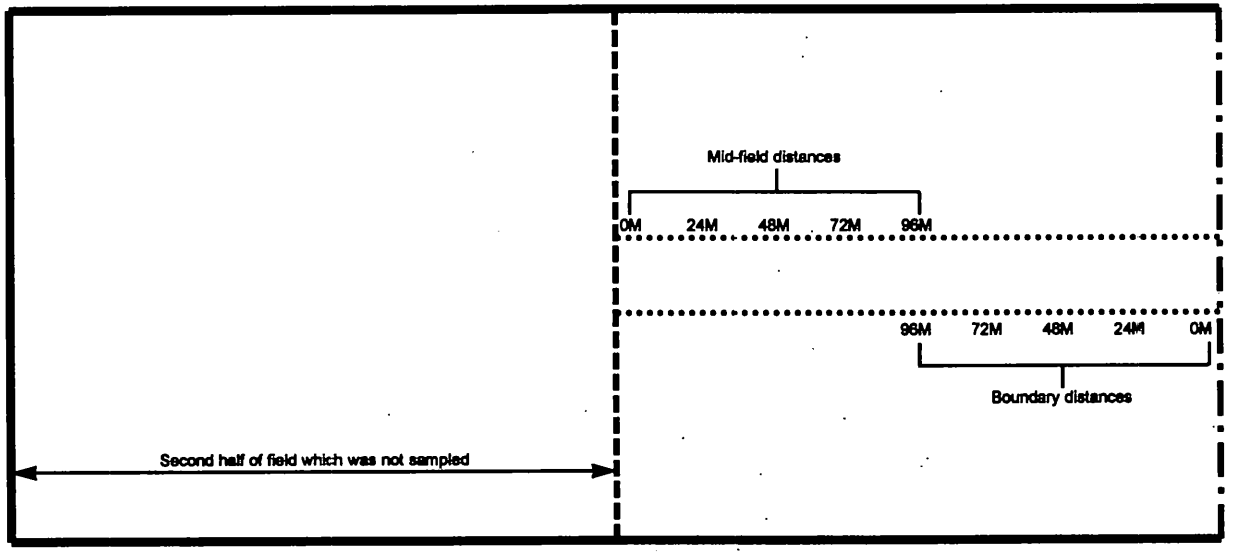
4.2.2 Monitoring polyphagous predator distribution in fields with and without beetle banks

Two transects were positioned in each field, running from the field boundary to either the beetle bank or to the centre of the field which had no beetle bank. In fields without beetle banks the centre of the field corresponded to the position of the beetle bank in the partner field. The transects were randomly positioned along the middle 50m of each field boundary, to minimise the influence of the other field boundaries (Fig. 14). Dietrick suction samples were taken and pitfall traps were placed at every 24m along each transect, to monitor polyphagous predator abundance and abundance/activity respectively. Two sampling points were also positioned in each field boundary and beetle bank.

One pitfall trap (8.5cm high and 6cm in diameter) containing ethylene glycol and detergent was placed at each sampling point along the transects. A rain cover was also fitted approximately 20cm above each trap. The traps were collected on a weekly basis between 3 April 1997 and 17 July 1997. All invertebrates collected were preserved in alcohol prior to identification.

Dietrick suction samples (D-vac) were taken alongside one of the transects (approximately 10m away) on a weekly basis. Five sub samples of ten seconds each ($0.46m^2$) were taken at each sampling site. Samples were taken on a weekly basis between 1 April 1997 and 8 July 1997. Suction samples could not be taken during wet weather and therefore data for some weeks are missing. Invertebrates sampled were frozen prior to being preserved in alcohol for identification at a later date.

Fig. 14. Schematic plan of the experimental design in fields with or without a beetle bank, exemplifying how the mid-field and boundary distances were calculated



KEY:-

:Beetle bank in fields with beetle banks or the middle of the field (ie. Where the beetle bank would be in the corresponding field containing a beetle bank) in fields without beetle banks

:Field Boundary along which transects were positioned

:Other field boundaries

:Transects positioned along the middle 50M of the field boundary

4.2.3 Analysis

The pitfall trap and D-vac data were analysed separately. Numbers of polyphagous predators caught in the pitfall traps were low, therefore the data were pooled into blocks of four weeks: 3 April – 24 April; 1 May – 22 May; 29 May – 19 June & 26 June – 17 July. The following taxonomic groups caught in pitfall traps during these months were analysed: total polyphagous predators, total Carabidae, 'boundary' type Carabidae, 'open-field' type Carabidae 'highly ranked boundary Carabidae', total Staphylinidae, *Tachyporus* species, Lycosidae and Linyphiidae. Numbers of predators caught in the D-vac samples were also low and it was impossible to pool the data from adjacent weeks because a large amount of data was missing due to bad weather preventing sampling. Only the following taxonomic groups were caught in high enough numbers for analysis: total polyphagous predators and total Staphylinidae.

The data were analysed using the field boundary as a within-field control for the mid-field. Firstly, the sum of the number of invertebrates from both transects was calculated at every mid-field and corresponding boundary distance from 0 to 96 metres, for each field with or without a beetle bank. The mid-field distance values were calculated by taking the first sampling point (ie. 0 metres) as either the centre of the cereal field or the beetle bank and working into the crop towards the field boundary from that point up to a distance of 96m. The boundary distance values were calculated using the field boundary as the first sampling point (ie. 0 metres) and working into the crop towards the centre of the field or the beetle bank, again up to a distance of 96m (Fig. 14).

Using these data, the ratio of each mid-field distance value to the corresponding boundary distance value was calculated for each field (see example). The regression slopes for each field with or without a beetle bank were then calculated using a regression of ratio against distance (both log transformed) for each field on a given date. The regression slopes were used in a paired t-test to discover whether the distribution of polyphagous predators differed significantly between fields with and without beetle banks on a given date.

Example: Total Staphylinidae caught in pitfall traps between 3 April & 24 April

Field 1 with a beetle bank

Distance (metres):	0m	24m	48m	72m	96m
Boundary distance values:	8	3	12	6	9
Mid-field distance values:	8	7	5	13	6
Ratio:	8:8	7:3	5:12	13:6	6:9

Field 1 without a beetle bank

Distance (metres):	0m	24m	48m	72m	96m
Boundary distance values:	6	8	2	5	2
Mid-field distance values:	2	13	2	9	2
Ratio:	2:6	13:8	2:2	9:5	2:2

It was hypothesised that the distribution of polyphagous predators in fields with and without beetle banks would change over time. To test this an ANOVA was performed on the regression slopes for each taxonomic group over time, using fields either with or without beetle banks as the factor. The relationship between the mean slope for each taxonomic group found in fields with or without beetle banks and the independent variable log distance was tested on each date separately using regression analysis. A non-significant result (ie. zero gradient) indicated that dispersal was independent of distance and predator distribution was uniform across the fields. A significantly positive gradient indicated that the size of the catch decreased with increasing distance away from the field boundary and vice versa for a significantly negative gradient. In fields with beetle banks a negative slope indicated that predators were emigrating from the beetle bank rather than the field boundary. Furthermore negative ratios indicated that the catch decreased with increasing distance from the field boundary and vice versa for positive ratios.

Overall it was hypothesised that the gradient for each taxonomic group in fields with beetle banks would approximate to zero faster than that in fields without beetle banks during the study period.

4.2.4 Assessment of the vegetation in the beetle banks and field margins of the fields under investigation

Ten random quadrats ($0.5m^2$) were used to assess the vegetational composition of the beetle banks and the field margins (where sampling points for polyphagous predators were placed). Samples were taken along each beetle bank and field margin and percentage ground cover of each species within the ground vegetation layer was estimated by eye.

4.3 RESULTS

4.3.1 Monitoring polyphagous predator distribution in fields with and without beetle banks

4.3.1.1 Pitfall trap results

Numbers of individual species caught in the pitfall traps were too low for analysis, however species caught in the traps were typical of those found on arable farmland.

4.3.1.1.1 Total polyphagous predators

There was no indication that the distribution of polyphagous predators differed significantly between fields with and without beetle banks (Table 14). Also the gradient of ratio versus distance did not vary significantly over time in either fields with or without beetle banks. The gradients in fields with beetle banks did not differ significantly from zero throughout the study indicating that total polyphagous predator density was fairly evenly distributed across the fields by April (Table 15). However, the mean gradients between April and early June in fields with beetle banks were negative (Table 16), which suggests that more predators were emigrating from the beetle bank than the field boundary, though not significantly so. Conversely the average gradient in fields without beetle banks was positive during the same time period (Table 16), though only significantly so at the beginning of the experiment in April (April 3 – 24) (Table 15). This indicated that the catch of polyphagous predators decreased with increasing distance away from the field boundary, particularly early in the season.

Table 14. Summary of paired t-test results (t values) investigating whether there were any significant differences (t_4) between the distribution of polyphagous predators found in pitfall traps in fields with and without beetle banks on each date (* P<0.05)

Taxonomic group	3 April – 24 April	1 May – 22 May	29 May – 19 June	26 June – 17 July
Total polyphagous predators	-2.20	-0.53	0.09	1.70
Carabidae				
Total	2.00	-0.12	0.48	2.23
'Boundary' type	-1.72	-1.44	0.43	1.84
'Open-field' type	0.21	0.33	-0.55	-0.53
'Highly ranked boundary'	-0.03	-0.79	-0.01	0.69
Staphylinidae				
Total	-1.45	2.34	4.40*	-0.56
Tachyporus species	-0.19	1.53	1.96	0.51
Araneae				
Linyphiidae	-0.04	-0.06	-0.72	1.54
Lycosidae	-4.02*	-1.12	-3.17*	-1.02

Table 15. Summary of regression results (t values) testing for zero gradient (t_{24}) for each of the taxonomic groups found in pitfall traps in fields with and without beetle banks on each date (* P<0.05) (+BB: fields with beetle banks; -BB: fields without beetle banks).

Taxonomic group	3 April – 24 April		1 May – 22 May		29 May – 19 June		26 June – 17 July	
	+ BB	- BB	+BB	-BB	+BB	-BB	+BB	-BB
Total polyphagous predators	-0.31	2.32*	-0.49	0.86	-0.29	-0.52	0.80	-1.19
Carabidae								
Total	0.86	0.24	-0.09	-0.31	-0.08	-1.47	1.09	-1.30
'Boundary' type	0.43	1.26	0.03	0.09*	-0.33	0.82	1.53	-0.47
'Open-field' type	0.21	-1.55	-0.33	-1.01	-0.57	-1.40	-0.39	-1.23
'Highly ranked boundary'	-0.05	1.00	-0.98	1.39	-0.34	-0.92	1.15	-
Staphylinidae								
Total	1.18	2.43*	0.72	-2.66*	1.97	-4.48*	0.08	0.23
Tachyporus species	-0.83	0.78	-0.75	-4.57*	0.27	-5.27*	-0.38	-1.60
Araneae								
Linyphiidae	0.26	3.11*	-0.42	0.19	-0.51	1.26	3.55*	-0.81
Lycosidae	-1.51	2.20	0.13	2.57*	-0.57	3.10*	-1.45	0.72

Table 16. Mean gradient for each taxonomic group found in pitfall traps in fields with and without beetle banks between April and July (+BB: fields with beetle banks; -BB: fields without beetle banks).

Taxonomic group	3 April – 24 April		1 May – 22 May		29 May – 19 June		26 June – 17 July	
	+ BB	- BB	+BB	-BB	+BB	-BB	+BB	-BB
Total polyphagous predators	-0.020	0.193	-0.036	0.036	-0.026	-0.035	0.070	-0.135
Carabidae								
Total	0.102	-0.149	-0.008	-0.021	-0.014	-0.201	0.131	-0.178
'Boundary' type	0.068	0.129	0.005	0.305	-0.058	0.125	0.241	-0.064
'Open-field' type	0.032	-0.211	-0.053	-0.090	-0.103	-0.218	-0.051	-0.172
'Highly ranked boundary'	-0.005	0.076	-0.203	0.152	-0.095	-0.156	0.242	-
Staphylinidae								
Total	0.010	0.215	0.077	-0.159	0.199	-0.236	0.012	0.031
Tachyporus species	-0.088	0.096	-0.128	-0.283	0.049	-0.367	-0.039	-0.222
Araneae								
Linyphiidae	0.030	0.248	-0.057	0.018	-0.051	0.105	0.229	-0.061
Lycosidae	-0.141	0.213	0.017	0.354	-0.129	0.562	-0.276	0.282

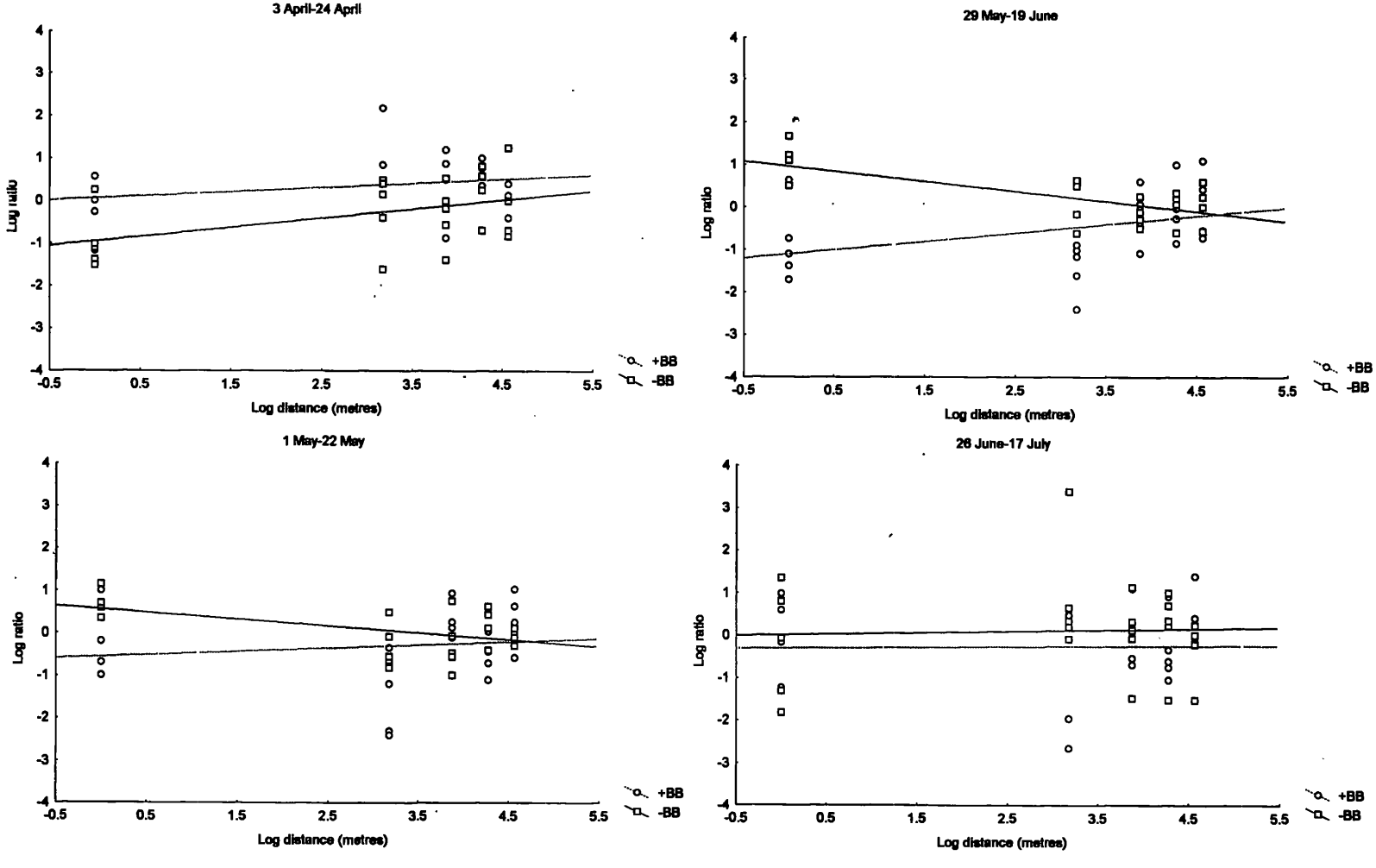
4.3.1.1.2 Carabidae

The distribution of all the carabids groups did not differ significantly between fields with and without beetle banks (Table 14). There was also no indication that the gradients of ratio against distance varied significantly with date for any of the carabid groups, either in fields with or without beetle banks. With the exception of the 'boundary' type Carabidae in fields without beetle banks, there were no significant non-zero gradients recorded for any of the carabid groups (Table 15), indicating that the Carabidae were fairly evenly distributed across fields with and without beetle banks by April. Although no significant results were obtained some general trends were observed. 'Open-field' type carabids dominated the Carabidae throughout the study. The gradients for the 'open-field' type carabids in fields with and without beetle banks were negative overall (Table 16). This indicated that more 'open-field' type carabids were caught with increasing distance from the field boundaries in fields without beetle banks and more 'open-field' type carabids were caught in the area surrounding the beetle bank in fields with beetle banks. Conversely the gradients for the 'boundary' type Carabidae were mainly positive in fields with and without beetle banks (Table 16), significantly so in fields without beetle banks between 1 May and 22 May (Table 15). These results indicated that the 'boundary' type Carabidae were more closely associated with the field boundary, though overall not significantly so. Interestingly between April and early June, the mean gradient for the 'highly ranked boundary carabids' was negative in fields with beetle banks (Table 16), suggesting that these carabids were emigrating in greater numbers from the beetle bank than from the field boundary.

4.3.1.1.3 Staphylinidae

The distribution of total Staphylinidae differed significantly between fields with and without beetle banks between 29 May and 19 June (Table 14). During this period significantly more Staphylinidae were caught at increasing distances away from the field boundary in fields without beetle banks (Fig. 15). Conversely in fields with beetle banks there were more Staphylinidae associated with the field boundary, though not significantly so (Table 15 & 16). The gradient of ratio against distance varied significantly with time in fields without beetle banks ($F_{3,16} = 5.96$, $p<0.01$). In these fields the gradients became increasingly negative between April and early June (Fig. 15 & Table 16). In April

Fig. 15. Mean regressions of log ratio (boundary distance values:mid-field distance values) versus log distance for the total number of Staphylinidae found in pitfall traps, in fields with (+BB) and without (-BB) beetle banks



significantly more Staphylinidae were caught near to the field boundary (Table 15). However between May and early June this trend reversed with significantly more Staphylinidae caught with increasing distance into the field (Table 15). By the end of June-early July the Staphylinidae were more evenly distributed across the fields (Fig. 15). Overall the gradients in fields with beetle banks were positive indicating that more Staphylinidae were caught near to the field boundary, though this was not significant (Tables 15 & 16). As for the fields without beetle banks a more even distribution of Staphylinidae was found in fields with beetle banks by the end of the study (Fig. 15).

Tachyporus hypnorum dominated the *Tachyporus* species. *Tachyporus* species distribution did not differ between fields with and without beetle banks (Table 14) and the gradients of ratio against distance did not vary significantly over time in either fields with or without beetle banks. In April the gradient in fields without beetle banks was positive indicating that the catch of *Tachyporus* species decreased with increasing distance from the field boundary, though not significantly (Table 15 & 16). This trend quickly reversed from May onwards when the gradient became negative (Table 16) suggesting that more *Tachyporus* species were caught with increasing distance into the field, significantly so between 1 May and 22 May, and 29 May and 19 June (Table 15). No gradients significantly different from zero were recorded in fields with beetle banks, indicating a more even distribution of *Tachyporus* species in these fields (Table 15). However the gradient was also negative in fields with beetle banks (Table 16), suggesting that more *Tachyporus* species were emigrating from the beetle bank than the field boundary and more *Tachyporus* species remained in the vicinity of the beetle bank, though not significantly so.

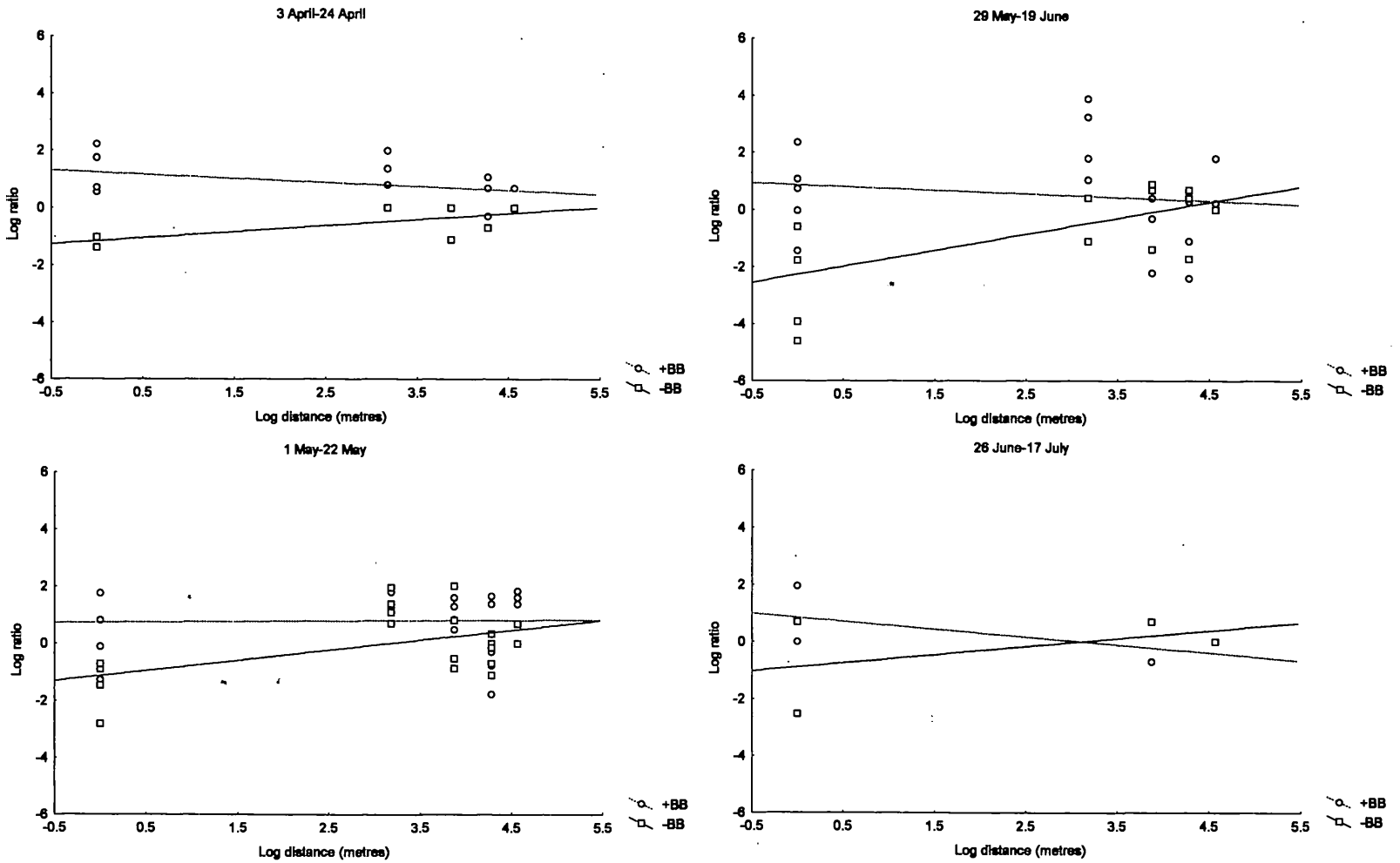
4.3.1.1.4 Araneae

The Linyphiidae dominated the Araneae catch. The distribution of linyphiids did not differ significantly between fields with and without beetle banks (Table 14) and the gradient of ratio versus distance did not vary significantly with time in either fields with or without beetle banks. During April the gradient was significantly positive in fields without beetle banks (Table 15 & 16), indicating that the catch of linyphiids decreased with increasing distance from the field boundary. During the same time period linyphiids were more evenly distributed across fields with beetle banks. By May the distribution of linyphiids was more evenly distributed in fields without beetle banks. However in fields with beetle banks the gradient became significantly positive in late June–early July (Table 15 & 16),

suggesting that the linyphiids were more closely associated with the field boundaries during this period.

The distribution of Lycosidae differed significantly between fields with and without beetle banks between 3 and 24 April, and 29 May and 19 June (Table 14). Overall Lycosidae were caught in greater numbers close to the field boundary in fields without beetle banks, significantly so between 1 May and 22 May, and 29 May and 19 June (Fig. 16 & Tables 15 & 16). The Lycosidae were more evenly distributed in fields with beetle banks, though there appeared to be more lycosids emigrating from the beetle banks compared to the field boundaries in April, and more lycosids in the vicinity of the beetle bank in late June- early July, but this was not significant (Fig. 16 & Tables 15 & 16).

Fig. 16. Mean regressions of log ratio (boundary distance values:mid-field distance values) versus log distance for the total number of Lycosidae found in pitfall traps, in fields with (+BB) and without (-BB) beetle banks



4.3.1.2 D-vac results

The abundance and diversity of polyphagous predators was vastly underestimated by the D-vac sampling technique. Sampling was also hindered by the wet weather, hence data for some dates are missing.

4.3.1.2.1 Total polyphagous predators

The distribution of predators differed significantly between fields with and without beetle banks on 22 April and nearly so on the 8 April ($p<0.05$) (Table 17). Overall the gradients in fields without beetle banks were positive indicating that the total number of polyphagous predators caught was greatest near to the field boundary, significantly so on 1 April, 8 April, 15 April, 22 April (nearly so on 27 May) and 10 June (Fig. 17 & Tables 18 & 19). Conversely between 1 April and 29 April the gradients were generally negative in fields with beetle banks (Table 19) indicating that more predators were emigrating from the beetle bank compared to the field boundary, though this was only significant on 8 April (Table 18). Between mid-April and harvest no gradients significantly different from zero were recorded in fields with beetle banks (Table 18), suggesting that total predator density was more evenly distributed in fields with beetle banks compared to fields without beetle banks (Fig. 17).

Table 17. Summary of paired t-test results (t values) investigating whether there were any significant differences (t_4) between the distribution of polyphagous predators caught in D-vac samples in fields with and without beetle banks on each date (* P<0.05).

Taxonomic group	1 April	8 April	15 April	22 April	29 April	27 May	3 June	10 June	8 July
Total polyphagous predators	-2.56	-2.78	-0.93	-5.14*	-2.51	-1.15	0.73	-2.07	0.74
Total Staphylinidae	-0.08	-2.54	-1.74	-2.12	-0.84	-0.98	-2.29	0.81	0.93

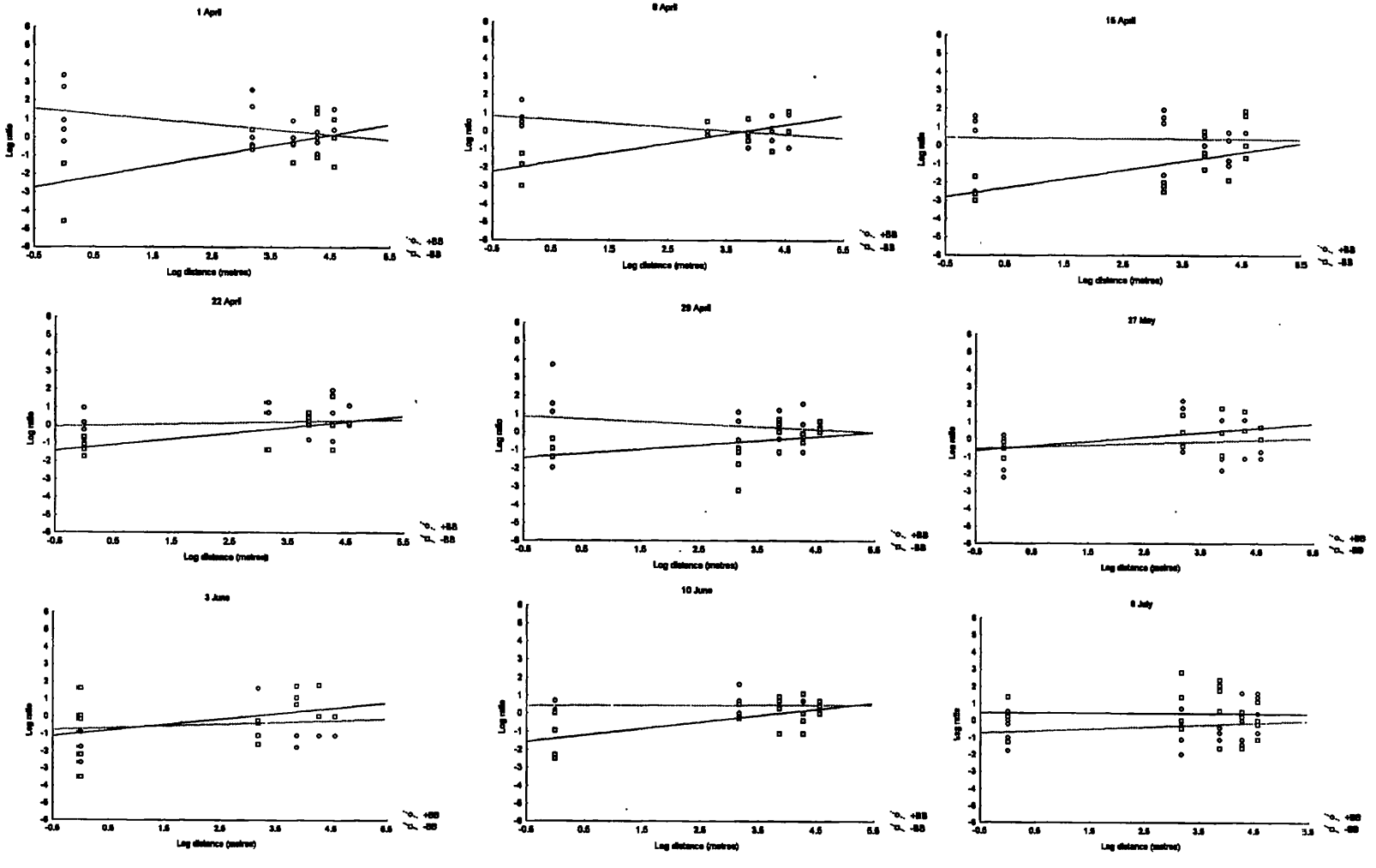
Table 18. Summary of regression results (t values) testing for zero gradient (t_{24}) for each of the taxonomic groups caught in D-vac samples in fields with and without beetle banks on each date (+BB: fields with beetle banks; -BB: fields without beetle banks) (* P<0.05).

Taxonomic group	1 April		8 April		15 April		22 April		29 April		27 May		3 June		10 June		8 July	
	+BB	-BB	+BB	-BB	+BB	-BB	+BB	-BB	+BB	-BB	+BB	-BB	+BB	-BB	+BB	-BB	+BB	-BB
Total polyphagous predators	-1.89	3.22*	-2.28*	4.38*	-0.09	2.82*	0.50	2.58*	-0.94	1.75	0.60	2.12	0.51	1.69	0.11	3.20*	0.98	-0.05
Total Staphylinidae	-0.36	2.42*	-2.46*	2.23	-1.35	1.30	-0.28	1.40	-0.60	0.55	0.36	0.78	-0.85	2.29*	0.06	0.53	-1.98	0.71

Table 19. Mean gradient for each taxonomic group caught in D-vac samples in fields with and without beetle banks between April and July (+BB: fields with beetle banks; -BB: fields without beetle banks).

Taxonomic group	1 April		8 April		15 April		22 April		29 April		27 May		3 June		10 June		8 July	
	+BB	-BB	+BB	-BB	+BB	-BB	+BB	-BB	+BB	-BB	+BB	-BB	+BB	-BB	+BB	-BB	+BB	-BB
Total polyphagous predators	-0.282	0.573	-0.201	0.514	-0.015	0.487	0.064	0.327	-0.147	0.231	0.009	0.255	0.105	0.320	0.008	0.360	0.117	-0.010
Total Staphylinidae	-0.060	0.427	-0.293	0.308	-0.153	0.234	-0.057	0.175	-0.074	0.074	0.067	0.082	-0.138	0.419	0.008	0.080	-0.353	0.181

Fig. 17. Mean regressions of log ratio (boundary distance values:mid-field distance values) versus log distance for the total number of polyphagous predators found in the D-vac samples, in fields with (+BB) and without (-BB) beetle banks



4.3.1.2.2 Total Staphylinidae

The distribution of Staphylinidae did not differ significantly between fields with and without beetle banks (Table 17), and the gradients of ratio against distance did not vary with date for fields with or without beetle banks. Overall the gradients were positive in fields without beetle banks indicating that more Staphylinidae were caught close to the field boundary, significantly so on the 1 April, (nearly so on 8 April $p<0.05$) and 3 June (Tables 18 & 19). Although only one significant negative gradient was recorded on 8 April for fields with beetle banks (Table 18), the gradients were negative overall during the study (Table 19). This suggested that more Staphylinidae were emigrating from the beetle banks compared to the field boundaries early in the season, and more Staphylinidae were staying in the vicinity of the beetle bank later in the year. These results contradict those from the pitfall trap results.

4.3.2 Assessment of the vegetation in the beetle banks and field margins of the fields under investigation

Results of the mean percentage ground cover (± one standard error) of the vegetation on the beetle banks and field margins are presented in Appendix VIII.ii-iv.

The beetle banks were mainly dominated by *Dactylis glomerata*, although the beetle banks in the fields labelled 1, 2, 4 and 5 also contained a high percentage of *Holcus lanatus*. Stands of *Phleum pratense* were also observed on the beetle banks in the fields labelled 1 and 4.

The vegetation in the field margins of the fields containing beetle banks was dominated by *Elytrigia repens*, with the exception of the field margin in the field containing a beetle bank labeled 5 which was dominated by *Arrhenatherum elatius*.

Arrhenatherum elatius also dominated the field margins in the fields without beetle banks labeled 1 and 3, whereas *Elytrigia repens* dominated the field margins in all the other fields without beetle banks. The field margin in field 4 without a beetle bank also contained a high percentage of *Galium aparine*.

4.4 DISCUSSION

The aim of this experiment was to investigate whether the inclusion of a beetle bank in cereal fields resulted in a more uniform distribution of predators through crops, earlier than in cereal fields with no beetle banks. It was particularly important to test this hypothesis for predatory groups which disperse mainly by walking, as it is the distribution of these predators that is most likely to be affected by the creation of large cereal fields. Surprisingly very few significant differences were found between fields with and without beetle banks in terms of polyphagous predator distribution in the crop. However several trends were recognisable for the different taxonomic groups.

Overall, analysis of all the predators combined indicated that the inclusion of a beetle bank in cereal fields can result in a more uniform distribution of predators through crops, compared to fields without beetle banks by early spring when aphid numbers are usually low and increasing slowly. Moreover, polyphagous predators were still more abundant in the vicinity of the field boundary in fields without beetle banks in early June, thus enabling aphid populations to grow unchecked in the centre of cereal fields. Only two of the taxonomic groups that contributed to the total namely, the Lycosidae and Staphylinidae, differed significantly in their distribution in fields with and without beetle banks. These two taxonomic groups comprise many different species, all of which have different ecological requirements and dispersal strategies. Unfortunately, it was not possible to analyse the distributions of individual species because numbers caught were too low for analysis. However, many of the Lycosidae and Staphylinidae recorded in this experiment have been found overwintering in field boundary habitats and beetle banks (Bayram & Luff, 1993; Chapter 2). As for all the predators combined, a more uniform distribution of Lycosidae was recorded by April in fields with beetle banks than in fields without beetle banks, where Lycosidae were caught in higher numbers near to field boundaries even during the summer. Several species of Lycosidae that are commonly found in arable fields also prey on cereal aphids (Nyfeller & Benz, 1988; Sunderland *et al.*, 1987a; Lang *et al.*, 1999). During the spring Lycosidae invade cereal crops mainly by walking, therefore the speed at which these predators can invade large fields is likely to be slower than that for predators which are active aeronauts, such as the linyphiids (Thomas, 1992). These results are encouraging as they suggest that by creating a beetle bank in cereal fields a more uniform distribution of Lycosidae can be achieved through the crop earlier in the spring than in fields without beetle banks.

Conversely, more Staphylinidae were caught with increasing distance away from the field boundary in fields without beetle banks during late May and early June, whereas Staphylinidae were more abundant close to the field boundary in fields with beetle banks during the same time period, though not significantly so. Overall, Staphylinidae only became relatively uniformly distributed in fields with and without beetle banks by late June-early July, when aphid populations are often well established. It was expected that the Staphylinidae would form a more even distribution in fields with and without beetle banks earlier than the results from this experiment suggested, as most staphylinids in the UK disperse by flying (Good & Giller, 1988). Pitfall traps are a measure of activity/abundance and many of the most abundant staphylinids in this study were not active until late summer, which may explain these results.

The distribution of all the other taxonomic groups, namely; Carabidae, 'boundary' and 'open-field' Carabidae, 'highly ranked boundary carabids', *Tachyporus* species and Linyphiidae, did not differ significantly between fields with and without beetle banks. With the exception of the 'boundary' carabids no gradients significantly different from zero were recorded for any of the carabid groups, indicating that their distribution was fairly uniform through the crop by April. Although many Carabidae disperse by flying, dispersal is dominated by walking in cereal fields (Coombes & Sotherton, 1986; Wallin & Ekbom, 1988; Thomas *et al.* , 1998). Some carabid species have the potential to cover large distance in one day by walking, for example *Pterostichus melanarius* (Wallin & Ekbom, 1988). However, the majority of these species are open-field type carabids which overwinter in the field rather than in boundary habitats. These carabids are therefore present throughout the crop during spring, though they are not usually abundant until late summer when the potential for polyphagous predators to prevent an aphid outbreak is lower (Edwards *et al.*, 1979; Chiverton, 1987). Therefore it is not surprising that no significant differences were obtained between fields with and without beetle banks in the distribution of 'open-field' type Carabidae. Conversely, 'boundary' type Carabidae which overwinter in boundary habitats are most active in early spring in cereal crops, when predator to prey ratios are higher and the potential to prevent an aphid outbreak is optimal (Edwards *et al.*, 1979; Coombes & Sotherton, 1986; Chiverton, 1987; Sunderland *et al.*, 1987a). However, Coombes and Sotherton (1986) showed that some of these carabids disperse in a slow wave from boundary overwintering sites into crops during the spring by walking. Therefore populations of these carabids may not be in sufficient numbers at field centres, particularly in large fields, at a time when aphid populations are increasing slowly.

Beetle banks aim to reduce the size of large fields, thus enabling these carabids to fully disperse through crops before the onset of an aphid invasion (Thomas *et al.*, 1991). Although the results from this experiment were difficult to interpret they indicated that 'boundary' type Carabidae appeared to be more closely associated with the field boundaries in fields with and without beetle banks during the study, though only significantly so in May in fields without beetle banks. Similar results were also obtained in the field experiment described in Chapter 3, where 'boundary' type Carabidae were generally more abundant in the vicinity of the beetle bank during the spring and summer. These data suggest that although beetle banks may aid the dispersal of these carabids through cereal crops, there appears to be an edge effect. Predator distribution in cereal crops may be influenced by a number of factors including prey distribution. Chambers *et al.* (1982) found that aphid populations are often higher in the middle of cereal fields. However, a recent study has shown that densities of aphids are often higher around the edges of cereal fields (Winder *et al.*, 1998). Other prey species may also be more abundant near to hedgebanks and beetle banks due to a number of factors, such as shelter provided by these habitats. The influence of prey distribution and other factors on predator distribution in cereal fields needs to be investigated further so that biological control strategies can be optimised.

The beetle bank appeared to be a good source of 'highly ranked boundary carabids' and *Tachyporus* species compared to the field boundaries in fields with beetle banks. Species belonging to these two taxonomic groups have been shown to overwinter in high densities in beetle banks and field boundaries (Thomas, 1991; Chapter 2). The 'highly ranked boundary carabids' (*Demetrias atricapillus*, *Agonum dorsale*, *Bembidion lampros*, *Amara plebeja* and *Amara familiaris*) are considered to be some the most important carabids in cereal aphid control (Sunderland & Vickerman, 1980). Many of these carabids disperse from overwintering sites into crops during the spring by walking, for example *Demetrias atricapillus*, *Bembidion lampros* and *Agonum dorsale* (Coombes & Sotherton, 1986). Therefore it was surprising that no significant differences were found between fields with and without beetle banks in terms of the distribution of these carabids. Coombes & Sotherton (1986) studied the dispersal of *Demetrias atricapillus*, *Bembidion lampros* and *Agonum dorsale* from a field boundary into a crop over a distance of 100 metres and found that dispersal was not complete until late May-early June. In this study 'the highly ranked boundary carabids' appeared to form a uniform distribution across cereal fields both with and without beetle banks by early April. However, the 'highly ranked boundary carabids'

were often caught in such low numbers during this study that significant differences may not have been detected and therefore these results should be viewed with caution.

Linyphiids and *Tachyporus* species disperse by ballooning and flying respectively and have the potential to disperse over a greater distance in a shorter space of time compared to predators that disperse by walking (Coombes & Sotherton, 1986; Thomas, 1992). For example, under the right weather conditions linyphiids can be redistributed from a field over a range of 1Km to 6Km downwind in a single day (Thomas, 1992). Therefore the inclusion of a beetle bank in cereal fields was expected to have less of an effect on the distribution of these taxonomic groups in the crop. However, there was some evidence to indicate that a more uniform distribution of linyphiids occurred in fields with beetle banks by April compared to fields without beetle banks, where linyphiids were caught in significantly higher numbers near the field boundaries. This trend reversed in late June-early July when more linyphiids were caught close to the field boundaries in fields with beetle banks, for reasons which are unknown. A pattern of dispersal away from the field boundaries into the crop was found for the *Tachyporus* species in fields without beetle banks between April and May. Whereas, the colonisation of fields with beetle banks by *Tachyporus* species appeared to be more rapid, with dispersal complete by April and no pattern of emigration discernable. The extra overwintering cover provided by the beetle banks in these fields, may have further enhanced the ability of these taxonomic groups to fully colonise cereal crops earlier than in fields without beetle banks. Linyphiids are particularly cold hardy (Foelix, 1982) and it is not known whether overwintering sites are an important key factor in the life cycle of these predators. However, many species of aphid eating linyphiids have been recorded on beetle banks and in field boundaries during winter (Chapter 2) and it has been suggested that populations of linyphiid spiders can be dramatically increased in cereal fields by including small amounts of grassland in arable landscapes (Halley *et al.*, 1996). These non-cropped habitats also provide a temporary refuge for linyphiids when fields are being ploughed or when pesticides are applied to crops (Halley *et al.*, 1996).

Overall the results from this experiment were not as expected, particularly for the Carabidae that overwinter in field boundary habitats. This may be explained by a number of intrinsic problems associated with this experiment. It is also advisable to view the results from this experiment with caution when taking into account the following problems. Firstly, very low numbers of predators were caught during the study. This made

analysis of the results particularly difficult and consequently may have been responsible for the low occurrence of significant results detected. Analysis of individual species would have been useful because only a few species of polyphagous predator are thought to be active early enough during spring and early summer to inhibit aphid population development (Edwards *et al.*, 1979; Coombes & Sotherton, 1986; Chiverton, 1987; Sunderland *et al.*, 1987a). Many of these predators also disperse from overwintering boundary habitats by walking, for example, *Demetrias atricapillus* (Coombes & Sotherton, 1986). However numbers of individual species caught were too low for analysis. Several of the problems associated with the techniques of pitfall trapping and suction sampling have already been discussed in Chapter 3. During this experiment only one pitfall trap was placed at each sampling point along the transects. The results indicated that more pitfall traps were needed to increase the catch of polyphagous predators, particularly of individual species. Capture efficiency could also have been increased by placing plastic edging vertically over a row of pitfall traps at each site (Holland, 1998). Barriers such as these are though to increase the capture efficiency of pitfall traps by guiding predators towards the trap (Durkis & Reeves, 1982).

As in Chapter 3, the D-vac technique proved to be inefficient for sampling many of the taxonomic groups and predator abundance and diversity was underestimated using this method. A major problem with the D-vac method in this experiment was that it could only be used in dry weather, when there was little moisture on the vegetation. Moisture on vegetation severely reduces the efficiency of vacuum samplers because invertebrates not only stick to the vegetation, but also to the sides of the collecting net. This impedes their removal from the net and can result in damage to delicate invertebrates making identification to species difficult or impossible (Sunderland *et al.*, 1995; Powell *et al.*, 1996). The spring and summer of 1997 was particularly wet hence D-vac sampling could not take place in some weeks, resulting in a great deal of missing data.

Several points should be taken into consideration when analysing data from pitfall trap and D-vac results, particularly when investigating predator dispersal in agricultural landscapes. For example, vegetation type and density not only affects the capture rates of pitfall traps but also affects the sampling efficiency of vacuum samplers (Sunderland *et al.*, 1995; Powell *et al.*, 1996). Vegetation type was not homogenous along the transects in the fields in this experiment and may therefore have affected the results. Consideration also needs to be given to aggregation. Some carabid beetles have been shown to aggregate in pitfall

traps, probably in response to aggregation or sex pheromones or defensive secretions (Luff, 1986). Other carabids have been found to aggregate in patches of high prey density (Bryan & Wratten, 1984). Prey density may also affect the activity of carabids in crops (Chiverton, 1984), thus affecting pitfall trap results which provide an indication of the activity/density of invertebrates (Sunderland *et al.*, 1995).

Secondly, crop type differed between fields, and in the fields with beetle banks labelled 1, 2 & 3 a different crop type was sown either side of the beetle bank. It is common practice for farmers to sow two different crop types either side of a beetle bank, rather than utilising the field as a whole for one crop (pers. obs.). Different crop types have their own structure, prey availability and husbandry practices which affect the diversity, abundance and guild structure of polyphagous predators in arable fields (Booji & Noorlander, 1992). Also the kind of crops grown in a rotation affect the occurrence of predators on arable land (Booji & Noorlander, 1992) and these rotations will have differed between the farms. Furthermore, predator abundance is affected by 'agroecological infrastructure', such as the spatial pattern of fields, crops, field margins, hedges and the natural environment (Sotherton, 1984; Bommarco, 1998; Thomas & Marshall, 1999). Again this will have varied considerably between farms and even fields on the same farm.

Rather than taking an extensive approach to studying predator dispersal in fields with and without beetle banks a more intensive approach could be applied. For example, a mark-recapture experiment conducted using grid sampling at regular intervals, over a certain period of time. Resulting data could be used to make estimates of dispersal rates, distances travelled and direction of movement from 'natural' (field boundaries) and semi-natural (beetle banks) overwintering habitats. Furthermore the grid system would enable detailed analysis of predator and prey spatial distribution in cereal crops over time, using recently introduced analytical procedures for analysing spatial data, such as SADIE (spatial analysis by distance indices) (Perry, 1995a & 1995b; Perry, 1996). However there are many problems associated with the method of mark-recapture, most notably that many species of interest are too small or delicate to be studied by this technique (Powell *et al.*, 1996; Thomas *et al.*, 1997). Furthermore, large numbers of invertebrates need to be caught and marked to ensure adequate re-capture rates, making this technique very labour intensive (Sunderland *et al.*, 1995).

A relatively new method the harmonic radar, could also be used to track the individual movements of predators from beetle banks into cereal crops. This may provide some idea of how far predators emigrating from beetle banks can penetrate cereal crops, enabling estimates of the optimal spacing of beetle banks in large cereal fields to be made. This study only investigated dispersal through cereal crops up to a distance of 96 metres. The results from this experiment indicated that many polyphagous predators are capable of fully colonising a field of this width by early spring when aphid populations are still in the establishing phase, however it would not be practical to space beetle banks this close in large cereal fields. Studies on the dispersal rates of linyphiids and large open-field inhabiting carabids, have indicated that these predators have the potential to fully disperse over greater distances than 96 metres in cereal fields by early spring (Wallin & Ekbom, 1988; Thomas, 1992; Thomas *et al.*, 1997; Thomas *et al.*, 1998). However, few experiments have investigated the dispersal rates of smaller boundary type Carabidae and other predators such as Lycosidae, which disperse mainly by walking. Since harmonic radar was first developed to track large (> 10mm) ground beetles, (Mascanzoni *et al.*, 1986) the size of the radar tag which is attached to the invertebrate has been reduced (Roland *et al.*, 1996). This has enabled the movements of much smaller invertebrates to be studied, for example bees (Riley *et al.*, 1996) and parasitic tachinid flies (Roland *et al.*, 1996). It may therefore be possible to use this technique to study the movements of some of the smaller important aphid-predators that disperse from beetle banks into crops during the spring. However, although these studies have shown that invertebrates appear to be unaffected by the tags, the real effect of the diode tags and antennae on invertebrate behaviour is unknown (Roland *et al.*, 1996; Thomas *et al.*, 1997).

In conclusion this study has indicated that the inclusion of a beetle bank in large cereal fields can result in a more uniform distribution of some predatory groups through crops, earlier than in fields without beetle banks. However, further studies are required to investigate what factors affect the process of field colonisation from beetle banks by polyphagous predators. Also, more detailed knowledge is needed about the dispersal rates and mobility of predators in agricultural landscapes and the effects of biotic and abiotic factors on predator distribution in cereal fields. This is particularly important for those predators that overwinter in 'natural' or semi-natural habitats, as the majority of work to date has concentrated on large open-field inhabiting carabids (Ericson, 1978; Wallin & Ekbom, 1988; Thomas *et al.*, 1997; Firle *et al.*, 1998; Thomas *et al.*, 1998). This information would result in a greater understanding of the role of beetle banks in

promoting the dispersal of predators through crops and the data could also be used to develop and parameterise simulation models of field colonisation from beetle banks by different predatory guilds and species.

CHAPTER 5.

GENERAL DISCUSSION

5.1 GENERAL DISCUSSION

Cereal aphids cause direct damage to cereal crops, resulting in reduced yields and grain quality (Wratten, 1975; Lee *et al.*, 1981; Oakley *et al.*, 1993; Oakley and Walters, 1994). It has been well documented that polyphagous predators have the potential to control cereal aphid populations (Edwards *et al.*, 1979; Sunderland & Vickerman, 1980; Sunderland *et al.*, 1987a; Chiverton, 1986; Holland & Thomas, 1997a), although this has rarely been demonstrated in the field. Many of these predators overwinter almost exclusively in field boundary habitats before migrating into crops during the spring (Sotherton, 1984 & 1985; Andersen, 1997). During the past 50 years, intensive farming practices have led to a reduction in the quality and abundance of these habitats on farmland (Boatman, 1989; Barr *et al.*, 1991; Sotherton, 1995). These and other factors associated with intensive farming systems, for example prophylactic spraying of broad-spectrum pesticides, have had a detrimental impact on polyphagous predator densities in cereal fields (Vickerman & Sunderland, 1977; Aebischer, 1991; Asteraki *et al.*, 1992; Greig-Smith *et al.*, 1992; Purvis & Bannon, 1992; Çilgi *et al.*, 1993). Furthermore, the creation of large fields for arable production reduces the boundary:field area ratio and therefore the final density of predators in crops may be lower than that in smaller fields (Thomas *et al.*, 1991). Moreover, in large fields predators that disperse by walking may still be in close association with field boundaries at the time of an aphid invasion (Coombes & Sotherton, 1986), enabling aphid populations to develop in the centre of the cereal fields in the absence of sufficient polyphagous predation.

Thomas *et al.* (1991) aimed to provide a solution to these problems by creating artificial overwintering habitats for polyphagous predators in the centre of cereal fields. These habitats are now commonly called beetle banks. Pioneering work conducted by Thomas (1991) on beetle banks in Hampshire during the early 1990s, indicated that these habitats could play a potentially important role in the biological control of cereal aphids. Tussocky grass species such as *Dactylis glomerata* that were sown on beetle banks supported densities of overwintering predators in excess of those found in surrounding good quality field margins (Thomas, 1991; Thomas *et al.*, 1991). Furthermore, beetle banks were shown to influence the dispersal of predators into the crop as a consequence of the reduction in field size. This resulted in a more uniform distribution of predators in cereal crops at a time when theoretically predator to prey ratios are still high and the potential for aphid control is optimal (Thomas, 1991; Thomas *et al.*, 1991). These studies led Thomas

et al. (1991) to suggest that 'enhanced' predator populations arising from beetle banks could prevent an aphid outbreak saving a total of £300 per year in labour and pesticide costs for a 20 ha field (Thomas *et al.*, 1991). Consequently beetle banks were promoted throughout the UK and abroad by The Game Conservancy Trust and are currently included in agri-environment schemes established by The Ministry of Agriculture, Fisheries and Food (MAFF), from which farmers can obtain grants for beetle banks on their land (MAFF, 1999a; MAFF, 1998c).

However, since these preliminary studies there has been little evidence to substantiate the potential agronomic benefits of beetle banks in cereal aphid control. Furthermore, there have been few studies to investigate whether similar results obtained from beetle banks in Hampshire can be replicated elsewhere, where environmental conditions such as soil type are different. Overwintering studies detailed in this thesis that were conducted in Leicestershire, indicated that beetle banks located elsewhere in the UK can support densities of overwintering predators similar to those reported from beetle banks in Hampshire (Thomas, 1991; McLeod, 1994). These studies also substantiated findings by Thomas (1991), that beetle banks sown with tussocky grass species (*Dactylis glomerata* and *Holcus lanatus*) provide an adequate habitat for overwintering predators by the first or second year after their creation, with densities of some of the most beneficial aphid predators similar to or greater than those in conventional field boundaries. Since the early investigations on beetle banks it has been questioned whether beetle banks actually enhance predator populations on farmland, or whether there is simply a re-distribution of predators within fields (Thomas *et al.*, 1991). Although further work is needed to verify this question, evidence cited in this thesis suggests that beetle banks do actually enhance predator populations in fields.

An investigation in this thesis examined five different grass species and a natural regeneration treatment, for their suitability in providing overwintering cover for polyphagous predators on beetle banks. Overall, the highest overwintering predator densities were recorded in grass species with tussocky growth forms and the lowest predator densities were recorded in treatments where the vegetation was allowed to naturally regenerate. *Dactylis glomerata* is particularly recommended for sowing on beetle banks, as this grass species supports high densities of those predators that disperse from overwintering sites into crops during spring by walking, in addition to supporting high densities of many other predators (Chapter 1). If techniques for augmenting predator

populations in cereal fields are to succeed, they need to be cheap to implement and easy to maintain. Although other tussocky grass species, such as *Arrhenatherum elatius* (Chapter 1) and *Holcus lanatus* (Thomas, 1991) have also been shown to support high densities of overwintering predators, seed for these grass species is difficult to obtain and is more expensive than that for *Dactylis glomerata*. However, where these species are found growing naturally in field boundaries they should be actively encouraged. Two other tussocky grass species that were found to be suitable for growing on beetle banks in this study were, *Phleum pratense* and *Festuca rubra*. An added advantage of *Festuca rubra* is that it has a creeping growth form and could be used in a mixture with *Dactylis glomerata* to fill in bare gaps often observed around the tussocks of this species, thereby minimising the potential for weed invasion on beetle banks. Topics for future research on beetle banks as overwintering sites for polyphagous predators could include, investigating whether the ability of grasses sown on beetle banks to support 'high' densities of polyphagous predators diminishes after a certain period of time.

The cost of creating a beetle bank of length 400m and width 2m, sown with either a mixture of *Dactylis glomerata* (20kg/ha) and *Festuca rubra* (10kg/ha) or a mixture of *Dactylis glomerata* (14kg/ha), *Festuca rubra* (10kg/ha) and *Phleum pratense* (6kg/ha), calculated using current seed prices (*D. glomerata* £6.00/kg; *F. rubra* £4.00/kg; *P. pratense* £5.00/kg (based on prices from a seed merchant)) and labour rates (total labour $2^{1/2}$ hours at £4.90/hour for a craft certificate grade 3 worker (Nix, 1998)), would be £25.05 and £24.57 respectively. Subsequent costs in maintaining a beetle bank would be small. For example, the only problem associated with the beetle banks in this study was invasion by thistles in some years, which was effectively resolved by spot spraying using a selective herbicide. However, the cost of creating and maintaining a beetle bank is minimal compared to the possible environmental and economic benefits of these habitats on arable farmland.

An experiment conducted in this thesis investigated the impact of polyphagous predators emigrating from a beetle bank on aphid populations in an adjacent crop of winter wheat. The effects of polyphagous predation were measured up to a distance of 83 metres into the crop from the beetle bank. The results indicated that polyphagous predators significantly reduced cereal aphid populations throughout the crop (Chapter 3), however the effects of polyphagous predation decreased with increasing distance from the beetle bank. The beetle bank also influenced the subsequent dispersal patterns of polyphagous predators into

the crop. Although some predatory groups showed a uniform dispersion throughout the crop by early spring, other predators remained in close association with the beetle bank during spring and summer. These findings were further substantiated by an experiment detailed in Chapter 4, which investigated the effect of the presence or absence of a beetle bank on the distribution of polyphagous predators in cereal crops. The impact of polyphagous predation on cereal aphid populations will vary from year to year depending upon factors such as, the timing and extent of aphid infestations (Edwards *et al.*, 1979; Chiverton, 1986 & 1987; Burn, 1992). This experiment was conducted in a year when the potential for polyphagous predators to prevent an aphid outbreak was low, due to the late infestation and rapid build up of the aphid population. Nevertheless, the results indicated that polyphagous predators were still capable of significantly reducing aphid populations in the crop up to a distance of 83 metres from the beetle bank. Results from the experiment conducted in Chapter 4, indicated that many polyphagous predators are capable of dispersing fully throughout a crop by early spring, over a distance of 96 metres into crops from beetle banks and field boundaries. Therefore it is possible that polyphagous predators may have a beneficial impact on aphid populations, at a greater distance than 83 metres into a crop from a beetle bank. However, it is not known whether the different levels of predation recorded throughout the crop in Chapter 3, would be sufficient to prevent an aphid outbreak in other years. Consequently, it is difficult to make recommendations based solely on this data about the spacing of beetle banks in arable fields to optimise the biological control of cereal aphids. Further studies to investigate what field density of polyphagous predators is required to prevent economic loss by cereal aphids and what factors affect the process of field colonisation from beetle banks by polyphagous predators, would help to answer this question.

Although these experiments cannot be used to quantify the economic effects of beetle banks, they have substantiated the hypothesis that beetle banks have a role to play in the biological control of cereal aphids. It is possible however to speculate on the cost-benefits of beetle banks in aphid control in winter wheat, by utilising current data on yields, grain prices, pesticide prices etc. To calculate the economic effects of a beetle bank it is necessary to consider two factors. Firstly, there is the loss of productive land, which is occupied by the beetle bank and secondly there are savings in the variable cost of insecticide use and application.

To exemplify the economic yield effects of a beetle bank in a crop of winter milling wheat, a bank of length 400m and width 2m situated in a field of 20ha was used in the cost-benefit analysis. The land occupied by the beetle bank would be 0.08ha, or alternatively 0.4% of the productive area. The current average yield for milling wheat is 7.05 tonnes per ha and the price approximately £80 per tonne (Nix, 1998). Therefore, a yield loss of 0.4% would result in an economic loss of £2.26/ha out of a total crop value of £564/ha. In the example of a 20ha field the yield loss would account for £45/year out of a total of £11, 280/year.

The variable cost of insecticide varies according to the season, type of control, number of applications required and policy employed on the farm. Average costs of about £3.40/ha/year have been predicted (Nix, 1998), though these may rise to £10/ha/year depending on the insecticide used. Total spray costs are currently estimated at £112/ha (herbicide, fungicide, insecticide and growth regulators), and total variable costs including sprays, fertiliser and seed are typically £240/ha (Nix, 1998). Insecticide costs are therefore only about 2% of variable costs, varying from 1% to 4%.

Table 20 shows a range of variable margins for winter milling wheat in 1999 based on information provided by Nix (1998), with an application of a cheap broad-spectrum organophosphorus insecticide, such as dimethoate (based on prices from 1998, provided by an agricultural merchant). An aphid population kept below spray threshold level by enhanced natural enemy populations, could save £6/ha in organophosphorus insecticide costs. Alternatively, if pyrethroid based insecticides or a more selective insecticide is used to control aphids, such as pirimicarb based insecticides, then approximately £10/ha and £11/ha could be saved respectively in costs. Although selective insecticides are more expensive than organophosphorus insecticides and to a lesser extent pyrethroid based insecticides they are less harmful to beneficial predators (Cole & Wilkinson, 1984). Consequently, an added advantage of these selective insecticides is that aphid resurgence is less likely because the background level of predation by polyphagous predators unharmed by the insecticide, may prevent aphid populations increasing once more. Furthermore, selective insecticides are less likely to unbalance other trophic relationships in agricultural ecosystems. For example, many farmland birds feed on invertebrates that are susceptible to the effects of organophosphorus insecticides such as dimethoate (Potts, 1986; Potts & Aebischer, 1995; Campbell & Cooke, 1997). Therefore where polyphagous predators are unable to prevent an aphid outbreak the use of a more selective insecticide is recommended.

Table 20. A summary of variable margins for winter milling wheat in 1999 based on information provided by Nix (1998), with an application of a cheap broad-spectrum organophosphorus insecticide, such as dimethoate (based on prices from 1998, provided by an agricultural merchant). Highlighted figures indicate predicted current costs.

Winter wheat (average for milling)			Without a beetle bank			
Yield/ha (Tonnes)	Crop value £/tonne	Insecticide £/ha	Cost of other sprays £/ha	Other variable costs £/ha	Area payments £/ha	Gross margin £/ha
7.05	110	6	106.5	127.5	242	778
	100	6	106.5	127.5	242	707
	90	6	106.5	127.5	242	637
	80	**6**	**106.5**	**127.5**	**242**	**566**
	70	6	106.5	127.5	242	496
	60	6	106.5	127.5	242	425
			With a beetle bank			
Yield/ha (Tonnes)	Crop value £/tonne	Insecticide £/ha	Cost of other sprays £/ha	Other variable costs £/ha	Area payments £/ha	Gross margin £/ha
7.05	110	-	106.5	127.5	242	784
	100	-	106.5	127.5	242	713
	90	-	106.5	127.5	242	643
	80	-	**106.5**	**127.5**	**242**	**572**
	70	-	106.5	127.5	242	502
	60	-	106.5	127.5	242	431

In the example of a beetle bank length 400m and width 2m in a 20ha field, the yield loss resulting from the presence of a beetle bank would reduce the gross margin by £2.26/ha, based on a current average yield of 7.05 tonnes/ha for milling wheat selling at £80/tonne. Allowing for this, an aphid population kept below spray threshold level by enhanced natural enemy populations, would therefore only save approximately £4/ha-£9/ha in costs depending on the insecticide used. The main economic effects of beetle banks will be on variable costs. The possible effects on fixed costs will vary considerably between farms. However, it is unlikely that there would be any significant savings in manpower, machinery or energy costs due to the presence of a beetle bank.

Grants for beetle banks are currently available in two agri-environment schemes run by MAFF, namely The Countryside Stewardship and Arable Stewardship Schemes (MAFF, 1999a; MAFF, 1998c). These schemes enable farmers to obtain grants of £15/100m/year for beetle banks on their land. The above calculations indicate that yield loss due to land being taken out of production is small and the money from these grants compensate this. However, there are limited funds available for these schemes and The Arable Stewardship Scheme is currently only being piloted in two areas of the UK, namely the West Midlands

and East Anglia (MAFF, 1998c). As mentioned previously although the yield loss element is small, the savings in insecticides though useful are also small. For example, even in the case of saving £11/ha on selective insecticide costs, the effect is small compared to the £240/ha total variable costs (Nix, 1998). These savings in insecticide costs may not be a big enough incentive to farmers unable to obtain grants to create beetle banks on their land. Furthermore, yield loss will increase if it is determined that more than one beetle bank is required to optimise bio-control in large cereal fields. However, there are many other additional benefits of beetle banks that may sway more environmentally aware farmers unable to obtain grants, into creating beetle banks on their land. For example, beetle banks are a means of increasing biodiversity in agricultural landscapes. As well as providing an excellent habitat for small mammals, in particular harvest mice (S. Bence, pers. comm.), a variety of wildflower mixes can be sown along with tussocky grasses on beetle banks to provide resources for bumble bees, butterflies and beneficial predators such as parasitoids and hoverflies. The latter may also increase the biological control potential of beetle banks. Beetle banks also harbour a wealth of invertebrate prey for farmland birds, many of which are in decline possibly as a result of a decrease in the abundance of invertebrate food on farmland, which is thought to be attributed to the effects of pesticides, in particular broad-spectrum organophosphorus insecticides (Potts, 1986; Potts & Aebischer, 1995; Campbell & Cooke, 1997). In the future it is envisaged that there will be an increase in land being used for valuable crops such as winter wheat and there will be a loss in set aside, which will reduce the potential benefits seen from its introduction, particularly in terms of biodiversity (MAFF, 1999b). Although beetle banks occupy only a small area of land their importance in sustaining biodiversity on farmland may increase as a result. The role of beetle banks in increasing biodiversity on farmland deserves further investigation.

Overall, there are potentially small but useful economic benefits of beetle banks in the biological control of cereal aphids, which need to be investigated further. However, when the potential environmental benefits are also considered, this makes beetle banks a valuable asset on farmland that should be positively encouraged.

In conclusion this research has shown that:

- Beetle banks sown with a mixture of *Dactylis glomerata* and *Holcus lanatus* can support densities of overwintering polyphagous predators, similar to or greater than those in conventional field margins by the second year of their establishment.

- Tussock forming grass species provide the best overwintering cover for polyphagous predators on beetle banks.

- Polyphagous predators emigrating from beetle banks can significantly reduce cereal aphid populations in winter wheat, though the impact of polyphagous predation appears to decrease with increasing distance from the beetle bank.

- Beetle banks aid the rapid colonisation of cereal fields by polyphagous predators in the early spring, when the potential for aphid control is optimal.

- There are potentially small but useful economic benefits of beetle banks in the biological control of cereal aphids, in terms of savings in insecticide costs.

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APPENDIX I

Latin names and authorities of all the flora and fauna mentioned in the thesis, including english names where applicable

Contents:

L.i Latin names and authorities of the flora mentioned in the thesis. English names given where applicable.

Latin name and authority	English name
Aethusa cynapium (Linnaeus)	Fool's Parsely
Agrostis stolonifera (Linnaeus)	Creeping Bent
Alopecurus geniculatus (Linnaeus)	Marsh Foxtail
Alopecurus myosuroides (Huds)	Black Grass
Anisantha sterilis (Linnaeus)	Barren Brome
Anthemis cotula (Linnaeus)	Stinking Chamomile
Arrhenatherum elatius (Linnaeus)	False Oat-grass
Atriplex patula (Linnaeus)	Common Orache
Avena fatua (Linnaeus)	Wild-oat
Brassica napus (Linnaeus)	Rape
Cerastium (Linnaeus) sp.	Mouse-ear sp.
Chrysanthemum leucanthemum (Linnaeus)	Oxeye Daisy
Cirsium arvense (Linnaeus)	Creeping Thistle
Cirsium palustre (Linnaeus)	Marsh Thistle
Cirsium vulgare (Savi)	Spear Thistle
Cynosurus cristatus (Linnaeus)	Crested Dog's Tail
Dactylis glomerata (Linnaeus)	Cock's-foot
Elytrigia repens (Linnaeus)	Common Couch
Festuca rubra (Linnaeus)	Red Fescue
Galium aparine (Linnaeus)	Cleavers
Geranium dissectum (Linnaeus)	Cut-leaved Crane's-bill
Glechoma hederacea (Linnaeus)	Ground-ivy
Heracleum sphondylium (Linnaeus)	Hogweed
Holcus lanatus (Linnaeus)	Yorkshire Fog
Hordeum (Linnaeus) sp.	Barley sp.
Lactuca serriola (Linnaeus)	Prickly Lettuce
Lamium album (Linnaeus)	White Dead-nettle
Lamium purpureum (Linnaeus)	Red Dead-nettle
Lolium multiflorum (Lam)	Italian Rye-grass
Lolium perenne (Linnaeus)	Perennial Rye-grass
Lolium x *boucheanum* (Kunth)	-
Lotus corniculatus (Linnaeus)	Comon Bird's-foot-trefoil
Matricarioides matricarioides (Less.)	Pineapple Weed
Myosotis arvensis (Linnaeus)	Field Forget-me-not
Papaver (Linnaeus) sp.	Poppy sp.
Pastinaca sativa (Linnaeus)	Wild Parsnip
Phleum pratense (Linnaeus)	Timothy
Poa annua (Linnaeus)	Annual Meadow Grass
Poa trivialis (Linnaeus)	Rough Meadow-grass
Polygonum aviculare (Linnaeus)	Knotgrass
Polygonum persicaria (Linnaeus)	Red Shank
Ranunculus repens (Linnaeus)	Creeping Buttercup
Rubus fruticosus (Linnaeus)	Blackberry Bramble
Rumex obtusifolius (Linnaeus)	Broad-leaved Dock
Senecio jacobaea (Linnaeus)	Common Ragwort
Senecio vulgaris (Linnaeus)	Groundsel
Sinapsis arvensis (Linnaeus)	Charlock
Sonchus oleraceus (Linnaeus)	Smooth Sow-thistle
Taraxacum officinale (Weber)	Common Dandelion
Trifolium pratense (Linnaeus)	Red Clover
Urtica dioica (Linnaeus)	Common Nettle

I. ii Latin names and authorities of the fauna mentioned in the thesis. English names given where applicable.

Order/Family,latin name and authority	English name
HEMIPTERA (Sub Order: HOMOPTERA)	
Aphididae	
Metopolophium dirhodum (Walker)	Rose Grain Aphid
Sitobion avenae (Fabricius)	Grain Aphid
Rhopalosiphum padi (Linnaeus)	Bird Cherry-oat Aphid
COLEOPTERA	
Carabidae	
Acupalpus meridianus (Linnaeus)	
Agonum dorsale (Pontoppidan)	
Agonum muelleri (Herbst)	
Amara aenea (De Geer)	
Amara apricaria (Paykull)	
Amara eurynota (Panzer)	
Amara familiaris (Duftschmid)	
Amara ovata (Fabricius)	
Amara plebeja (Gyllenhal)	
Amara similata (Gyllenhal)	
Bembidion aeneum (Germar)	
Bembidion guttula (Fabricius)	
Bembidion lampros (Herbst)	
Bembidion obtusum (Serville)	
Bembidion quadrimaculatum (Linnaeus)	
Bradycellus harpalinus (Serville)	
Bradycellus verbasci (Duftschmid)	
Clivina fossor (Linnaeus)	
Demetrias atricapillus (Linnaeus)	
Dromius linearis (Olivier)	
Dromius melanocephalus (Dejean)	
Harpalus aeneus (Fabricius)	
Harpalus rufipes (De Geer)	
Notophilus biguttatus (Fabricius)	
Pterostichus cupreus (Linnaeus)	
Pterostichus melanarius (Illiger)	
Pterostichus niger (Schaller)	
Pterostichus strenuus (Panzer)	
Pterostichus vernalis (Panzer)	
Trechus quadristriatus (Schrank)	
Staphylinidae	
Philonthus cognatus (Stephens)	
Tachyporus chrysomelinus (Linnaeus)	
Tachyporus hypnorum (Fabricius)	
Tachyporus obtusus (Linnaeus)	

I. ii Latin names and authorities of the fauna mentioned in the thesis continued.

Order/Family,latin name and authority	English name
ARANEAE	
Clubionidae	
Clubiona diversa (O. P. Cambridge)	
Clubiona lutescens (Westring)	
Linyphiidae	
Bathyphantes gracilis (Blackwall)	
Centromerita bicolor (Blackwall)	
Centromerita concinna (Thorell)	
Dicymbium nigrum (Blackwall)	
Diplostyla concolor (Wider)	
Erigone atra (Blackwall)	
Erigone dentipalpis (Wider)	
Gongylidiellum vivum (O. P. Cambridge)	
Lepthyphantes ericaeus (Blackwall)	
Lepthyphantes tenuis (Blackwall)	
Meioneta rurestris (C. L. Koch)	
Micrargus herbigradus (Blackwall)	
Neriene clathrata (Sundevall)	
Oedothorax apicatus (Blackwall)	
Oedothorax fuscus (Blackwall)	
Oedothorax retusus (Westring)	
Oetearius melanopygius (O. P. Cambridge)	
Porrhomma microphthalmum (O. P. Cambridge)	
Savignya frontata (Blackwall)	
Walckenaeria acuminata (Blackwall)	
Walckenaeria nudipalpis (Westring)	
Walckenaeria unicornis (O.P. Cambridge)	
Lycosidae	
Pardosa amentata (Clerck)	
Pardosa prativaga (L. Koch)	
Trochosa ruricola (Degeer)	
Mimetidae	
Ero cambridgei (Kulczynski)	
Tetragnathidae	
Pachygnatha clercki (Sundevall)	
Pachygnatha degeeri (Sundevall)	
Thomisidae	
Xysticus cristatus (Clerck)	

Appendix II

Tabulated representation of the linear randomised block design of the treatments sown on the beetle banks (section 2.2.2)

Beetle bank 1		
Block	Plot	Treatment
A	1	Fr
A	2	Nr
A	3	Dg / Fr
A	4	Ae / Fr
A	5	Pp
A	6	Ae
A	7	C5
A	8	Dg
A	9	Cc
A	10	Dg / Hl
B	1	Ae / Fr
B	2	Dg / Fr
B	3	Cc
B	4	Ae
B	5	Pp
B	6	Nr
B	7	Fr
B	8	Dg
B	9	Dg / Hl
B	10	C5

Beetle bank 2		
Block	Plot	Treatment
C	1	Cc
C	2	Dg / Fr
C	3	Pp
C	4	Ae / Fr
C	5	Ae
C	6	Fr
C	7	Dg
C	8	Dg / Hl
C	9	C5
C	10	Nr
D	1	Fr
D	2	Nr
D	3	Ae / Fr
D	4	Dg
D	5	Dg / Hl
D	6	Ae
D	7	C5
D	8	Cc
D	9	Pp
D	10	Dg / Fr

Key:

Dg = *Dactylis glomerata*

Fr = *Festuca rubra*

Cc = *Cynosurus cristatus*

Ae = *Arrhenatherum elatius*

Pp = *Phleum pratense*

Nr = Natural regeneration

Ae / Fr = *A. elatius* and *F. rubra*

Dg / Hl = *D. glomerata* and *Holcus lanatus*

Dg / Fr = *D. glomerata* and *F. rubra*

C5 = Cotswald 5 species mix

APPENDIX III

Carabid and Araneae species composition in the beetle bank (section 2.3.1) between the winters 1993 & 1997

Contents:

III.i Carabid species found overwintering within the beetle bank (section 2.3.1) over the five year study period. * indicates presence of a species; B = boundary type; F = open-field type; - = unknown overwintering strategy

III. ii Araneae species found overwintering within the beetle bank (section 2.3.1) between 1994 & 1997: * indicates presence of a species

III.i Carabid species found overwintering within the beetle bank (section 2.3.1) over the five year study period. * indicates presence of a species; B = boundary type & F = open- field type (Desender, 1982; Sotherton, 1984 & 1985; Andersen, 1997; M.L. Luff, pers. comm)

	Winter	Year				
Carabid		1993	1994	1995	1996	1997
Acupalpus meridianus	B					*
Agonum dorsale	B			*		
Agonum muelleri	B			*		
Amara apricaria	F				*	
Amara eurynota	F					*
Amara familiaris	B			*		*
Amara plebeja	B			*	*	*
Bembidion guttula	B		*	*	*	*
Bembidion lampros	B			*	*	*
Bembidion obtusum	F		*	*	*	
Bembidion spp.	-	*				
Bradycellus harpalinus	B			*		
Bradycellus verbasci	F			*		*
Clivina fossor	F/B			*	*	*
Demetrias atricapillus	B			*	*	*
Dromius linearis	B	*			*	
Dromius melanocephalus	B					*
Pterostichus melanarius	F				*	
Pterostichus niger	B			*		
Pterostichus strenuus	B			*	*	*
Pterostichus vernalis	B			*		
Trechus quadristriatus	F			*	*	*
N° of Genera		2	1	8	7	9

III. ii Araneae species found overwintering within the beetle bank (section 2.3.1) between 1994 & 1997: * indicates presence of a species

Species	Year			
	1994	1995	1996	1997
Bathyphantes gracilis	*			*
Centromerita bicolor			*	*
Centromerita concinna	*			
Diplostyla concolor		*		*
Micrargus herbigradus		*		
Neriene clathrata			*	
Oedothorax retusus	*			
Savignya frontata		*		
Walckenaeria nudipalpis		*		
Walckenaeria unicornis			*	
Ero cambridgei		*		*
Pachygnatha clercki		*		*
Pisaura mirabilis			*	
Clubiona sp.			*	*
Oxyptila sp.			*	
Pardosa sp.			*	*
Trochosa sp.			*	*

APPENDIX IV

Vegetation data for the beetle bank and hedgebanks in section 2.3.1

Contents:

IV. i Mean percentage ground cover ± one standard error of the beetle bank (section 2.3.1) in the summers of 1993, 1994, 1996 & 1997

	Year			
Species	1993	1994	1996	1997
Anthemis cotula	0.25 ± 0.25	0	0	1 ± 0.75
Atriplex patula	0.38 ± 0.38	0	0	0
Avena fatua	10 ± 2.51	0	0	0
Bare ground	3 ± 1.16	12 ± 1.55	4 ± 1.32	1 ± 0.65
Brassica napus	0.13 ± 0.13	0	0	0
Cerastium sp.	0.5 ± 0.50	0	0	0
Cirsium palustre	0.25 ± 0.25	0	0	0
Cirsium vulgare	0	0	4 ± 2.24	1 ± 0.64
Dactylis glomerata	39 ± 4.64	57 ± 3.31	73 ± 4.25	68 ± 4.12
Elytrigia repens	1 ± 0.70	0	0	1 ± 0.42
Galium aparine	1 ± 0.64	0	4 ± 1.29	14 ± 2.89
Holcus lanatus	35 ± 4.02	13 ± 2.64	5 ± 2.53	7 ± 3.27
Litter	0	18 ± 1.37	7 ± 2.54	0
Lolium perenne	0.25 ± 0.17	0	0	0
Myosotis arvensis	0	0	2 ± 0.55	7 ± 1.89
Poa trivialis	0	0	1 ± 1.03	0
Polygonum aviculare	13 ± 3.34	0	0	0
Polygonum persicaria	7 ± 1.62	0	0	0
Senecio jacobaea	0	0	1 ± 0.45	0
Weeds	0	1 ± 0.58	0	0

IV. ii Mean percentage ground cover ± one standard error of hedgebank 1 in the summers of 1996 & 1997

Species	Year	
	1996	1997
Agrostis stolonifera	1 ± 1.02	0
Alopecurus myosuroides	2 ± 1.50	2 ± 1.50
Anthemis cotula	0	3 ± 2.50
Arrhenatherum elatius	18 ± 6.65	26 ± 7.67
Avena fatua	0	0.5 ± 0.50
Bare ground	1 ± 0.55	0.3 ± 0.30
Cirsium arvense	0	6 ± 4.20
Cirsium vulgare	0.8 ± 0.80	0.3 ± 0.30
Dactylis glomerata	7 ± 4.99	0
Elytrigia repens	23 ± 7.21	32 ± 7.99
Anisantha sterilis	2 ± 1.75	0
Festuca rubra	1 ± 1.00	0
Galium aparine	16 ± 5.49	1 ± 0.71
Holcus lanatus	8 ± 4.21	7 ± 3.57
Lamium album	4 ± 2.57	7 ± 4.59
Lamium purpureum	0	4 ± 2.45
Lolium perenne	0.3 ± 0.30	0
Mysotis arvensis	0	6 ± 2.81
Ranunculus repens	6 ± 3.26	0
Rubus fruticosus	4 ± 2.54	2 ± 0.92
Rumex obtusifolius	1 ± 0.79	1 ± 0.55
Sonchus oleraceus	0	18 ± 15.08

IV. iii Mean percentage ground cover ± one standard error of hedgebank 2 in the summers of 1996 & 1997

Species	Year	
	1996	1997
Agrostis stolonifera	3 ± 1.28	0
Alopecurus myosuroides	2 ± 1.26	1 ± 0.34
Arrhenatherum elatius	13 ± 6.07	14 ± 6.53
Avena fatua	0.3 ± 0.30	0.3 ± 0.30
Bare ground	1 ± 0.80	1 ± 1.02
Dactylis glomerata	2 ± 1.75	4 ± 4.00
Elytrigia repens	76 ± 6.02	67 ± 8.06
Festuca rubra	1 ± 0.80	4 ± 2.76
Galium aparine	0	2 ± 1.38
Heracleum sphondylium	1 ± 1.00	0.5 ± 0.50
Holcus lanatus	0.1 ± 0.10	0
Lamium album	1 ± 0.58	3 ± 1.59
Lamium purpureum	0	3 ± 3.00
Matricaria matricarioides	0.8 ± 0.80	0
Mysotis arvensis	0	0.3 ± 0.30
Poa trivialis	0.1 ± 0.10	0

IV. iv Mean percentage ground cover ± one standard error of the soil cores taken from the beetle bank (section 2.3.1) in the winters of 1993, 1994, 1995, 1996 & 1997

Species	Year				
	1993	1994	1995	1996	1997
Bare ground	2 ± 0.71	26 ± 7.83	5 ± 3.32	0	0
Broad leaved weeds	0	3 ± 1.44	0	0	0
Dactylis glomerata	56 ± 10.18	18 ± 6.89	90 ± 4.69	88 ± 5.02	100 ± 0.00
Elytrigia repens	4 ± 2.05	0	0	0	0
Holcus lanatus	25 ± 6.92	6 ± 4.34	5 ± 3.49	0	0
Litter	0	46 ± 7.01	0	12 ± 5.02	0
Moss	0	1 ± 0.90	0	0	0
Other Gramineae	0	0.8 ± 0.83	0	0	0
Polygonum aviculare	10 ± 5.31	0	0	0	0
Polygonum persicaria	4 ± 2.96	0	0	0	0

IV. v Mean percentage ground cover ± one standard error of soil cores taken from hedgebank 1 in the winters of 1993, 1995, 1996 & 1997

	Year			
Species	1993	1995	1996	1997
Alopecurus myosuroides	0	16 ± 5.20	0	0
Atriplex patula	2 ± 2.00	0	0	0
Bare ground	5 ± 2.00	11 ± 4.35	9 ± 3.82	0
Brassica napus	0	0.13 ± 0.13	0	0
Cerastium sp.	0	0.13 ± 0.13	1 ± 1.00	0
Dactylis glomerata	0	5 ± 3.40	3 ± 3.00	0
Elytrigia repens	66 ± 9.64	8 ± 3.66	43 ± 7.60	92 ± 4.14
Festuca rubra	0	0	0	3 ± 3.00
Galium aparine	7 ± 2.92	14 ± 4.23	1 ± 1.00	0.13 ± 0.13
Glechoma hederacea	0	0	0	0
Heracleum sphondylium	0	0	1 ± 1.00	0
Humus	0	7 ± 4.16	0	0
Lamium album	0	1 ± 0.51	0	0
Lamium purpureum	10 ± 5.26	0	0	0
Litter	0	26 ± 6.41	37 ± 7.27	3 ± 2.38
Moss	0	10 ± 4.35	0	0
Poa annua	0	2 ± 0.76	0	0
Poa trivialis	9 ± 5.04	0	3 ± 3.00	3 ± 3.00
Ranunculus repens	0	0.40 ± 0.28	2 ± 0.97	0
Urtica dioica	0	0	1 ± 1.00	0

IV. vi Mean percentage ground cover ± one standard error of soil cores taken from hedgebank 2 in the winters of 1993, 1994, 1995, 1996 & 1997

	Year				
Species	1993	1994	1995	1996	1997
Alopecurus myosuroides	0	0	0	0	0
Bare ground	11 ± 3.91	21 ± 6.90	4 ± 3.10	1 ± 1.00	0
Dactylis glomerata	0	0	1 ± 1.00	10 ± 6.88	0
Dicotyledon litter	0	10 ± 5.24	0	0	0
Elytrigia repens	72 ± 6.23	37 ± 7.52	17 ± 6.07	83 ± 8.03	100 ± 0.10
Festuca rubra	0	0	5 ± 5.00	0	0
Galium aparine	3 ± 0.94	0	0	0	0
Lamium album	0	0	0.25 ± 0.25	0	0
Litter	0	0	29 ± 9.15	6 ± 4.98	0.1 ± 0.10
Monocotyledon litter	0	33 ± 5.31	0	0	0
Moss	0	0	0.25 ± 0.25	0.25 ± 0.25	0
Poa annua	0	0	1 ± 1.00	0	0
Poa trivialis	6 ± 3.85	0	0	0	0
Rubus fruticosus	2 ± 1.00	0	0	0	0
Urtica dioica	5 ± 2.89	0	0	0	0

IV. vii Mean visimeter recordings for the beetle bank (section 2.3.1) in the winters of 1993, 1995 & 1997

Height category (cm)	Percentage vertical cover ± one standard error		
	1993	1995	1997
0-5	61 ± 4.85	83 ± 2.72	89 ± 1.98
5-10	35 ± 5.23	72 ± 3.30	73 ± 3.38
10-20	16 ± 4.03	56 ± 3.58	49 ± 3.69
20-30	7 ± 2.55	44 ± 3.59	25 ± 3.14
30-40	1 ± 0.50	33 ± 3.29	11 ± 2.27
40-50	0	22 ± 2.68	6 ± 1.66
50-60	0	15 ± 2.17	4 ± 1.28
60-70	0	11 ± 1.83	2 ± 0.87
70-80	0	7 ± 1.40	1 ± 0.62
80-90	0	4 ± 1.04	1 ± 0.61
90-100	0	3 ± 0.82	1 ± 0.60

IV.viii Mean visimeter recordings for hedgebank 1 & 2 in the winter of 1997

Height category (cm)	Percentage vertical cover ± one standard error	
	Hedgebank 1	Hedgebank 2
0-5	57 ± 3.46	60 ± 4.46
5-10	44 ± 3.72	37 ± 5.07
10-20	27 ± 3.12	12 ± 3.14
20-30	12 ± 2.14	2 ± 1.11
30-40	5 ± 1.28	0.3 ± 0.26
40-50	3 ± 0.88	0.01 ± 0.01
50-60	1 ± 0.41	0.01 ± 0.01
60-70	0.7 ± 0.34	0.01 ± 0.01
70-80	0.6 ± 0.29	0
80-90	0.5 ± 0.29	0
90-100	0.1 ± 0.13	0

APPENDIX V

Carabid and Araneae species composition in the beetle banks in section 2.3.2.

Contents:

V.i Carabid species found overwintering within the six treatments (section 2.3.2) over the four year study period. * indicates presence of a species; B = boundary type; F = open-field type; - = unknown overwintering strategy

V. ii Araneae species found overwintering within the six treatments (section 2.3.2) over the four year study period * indicates presence of a species

V.i Carabid species found overwintering within the six treatments (section 2.3.2) over the four year study period. * indicates presence of a species; B = boundary type; F = open- field type; - = unknown overwintering strategy (Desender, 1982; Sotherton, 1984 & 1985; Andersen, 1997; M.L. Luff, pers. comm)

Carabid	Winter habitat	Year			
		1994	1995	1996	1997
Acupalpus meridianus	B				*
Agonum dorsale	B	*			*
Amara aenea	F		*		
Amara apricaria	F		*	*	
Amara eurynota	F				*
Amara familiaris	B		*	*	*
Amara ovata	F	*			
Amara plebeja	B	*	*	*	*
Amara similata	F	*	*		
Bembidion aeneum	B	*			
Bembidion guttula	B	*	*	*	*
Bembidion lampros	B	*	*	*	*
Bembidion obtusum	F	*	*	*	*
Bembidion quadrimaculatum	B	*			
Bradycellus harpalinus	B		*	*	*
Bradycellus verbasci	F				*
Clivina fossor	F/B	*	*		*
Demetrias atricapillus	B	*	*	*	*
Dromius linearis	B		*		
Dromius melanocephalus	B		*	*	*
Harpalus aeneus	F		*		
Harpalus rufipes	B		*		*
Notophilus biguttatus	F	*			
Pterostichus cupreus	F/B				*
Pterostichus melanarius	F				*
Pterostichus strenuus	B	*			*
Trechus quadristriatus	F	*	*	*	*
N° of genera		8	8	6	11

V.ii Araneae species found overwintering within the six treatments (section 2.3.2) over the four year study period. * indicates presence of a species

Species	Year			
	1994	1995	1996	1997
Bathyphantes gracilis	*			*
Centromerita bicolor	*	*	*	*
Dicymbium nigrum	*	*	*	*
Diplostyla concolor	*	*		*
Erigone atra	*			
Gongylidiellum vivum		*		
Lepthyphantes ericaeus			*	
Lepthyphantes tenuis	*			
Meioneta rurestris	*		*	*
Micrargus herbigradus		*	*	*
Oedothorax apicatus	*		*	
Oedothorax fuscus	*			
Oedothorax retusus	*			
Ostearius melanopygius	*			
Porrhomma microphthalmum	*			
Walckenaria acuminata			*	
Walckenaria mudipalpus			*	*
Clubiona diversa			*	
Clubiona lutescens			*	
Clubiona sp.			*	*
Ero cambridgei	*			
Ero sp.				*
Pachygnatha degreei	*	*	*	*
Pachygnatha clercki				*
Tetragnatha sp.				*
Tibellus sp.			*	*
Xysticus cristatus			*	
Xysticus sp.				*
Zora sp.				*
Aleopecosa sp.				*
Pardosa sp.	*	*	*	*
Pisaura mirabilis			*	
Trochosa ruricola	*	*		
Trochosa sp.			*	*

APPENDIX VI

Vegetation data for the beetle banks in section 2.3.2

Contents:

VI. i Mean percentage ground cover ± one standard error in tho *Cynosurus cristatus* treatment in the summers of 1994, 1995, 1996 & 1997

Species	Year			
	1994	1995	1996	1997
Agrostis stolonifera	0	0	0	0.3 ± 0.30
Alopecurus myosuroides	0	3 ± 1.02	0.4 ± 0.28	6 ± 1.61
Alopecurus sp.	0.2 ± 0.20	0	0	0
Anthemis cotula	0	0	1 ± 0.67	2 ± 1.04
Arrhenatherum elatius	0	0	2 ± 0.85	2 ± 0.68
Avena fatua	11 ± 1.22	10 ± 2.06	0	2 ± 0.77
Bare ground	20 ± 1.75	3 ± 1.26	1 ± 0.76	1 ± 0.37
Brassica napus	0	0	0	1 ± 1.00
Cirsium arvense	0	0	0	2 ± 0.92
Cirsium vulgare	0	0	13 ± 3.11	0
Cynosurus cristatus	10 ± 1.44	36 ± 4.03	43 ± 4.91	9 ± 2.46
Dactylis glomerata	1 ± 0.46	0.1 ± 0.10	1 ± 1.00	3 ± 2.51
Elytrigia repens	0	4 ± 1.26	2 ± 1.40	31 ± 5.85
Festuca rubra	0.3 ± 0.23	0	7 ± 2.80	18 ± 4.25
Festuca sp. a	0	0	0.03 ± 0.03	0
Festuca sp. b	0	0	0	0
Galium aparine	0	0	0.3 ± 0.30	0.3 ± 0.30
Geranium dissectum	0	0	2 ± 1.18	1 ± 0.61
Holcus lanatus	0	1 ± 1.00	1 ± 1.00	4 ± 1.54
Hordeum sp.	0	0.03 ± 0.03	0	0
Lolium perenne	1 ± 0.62	0	0	0
Lolium sp.	0	0	3 ± 1.29	7 ± 2.33
Myosotis arvensis	0	0	1 ± 0.62	0
Phleum pratense	0	1 ± 0.80	0.3 ± 0.3	1 ± 1.00
Poa annua	2 ± 2.31	8 ± 1.80	0	0
Poa trivialis	20 ± 2.31	24 ± 2.92	20 ± 3.43	3 ± 1.40
Ranunculus repens	0	7 ± 2.85	1 ± 0.63	1 ± 0.67
Rumex obtusifolius	0	1 ± 1.00	2 ± 1.26	6 ± 2.74
Senecio jacobaea	0	0	0	1 ± 1.00
Senecio vulgaris	0	0	0	0.3 ± 0.30
Sinapis arvensis	24 ± 2.77	0	2 ± 0.83	0
Sonchus oleraceus	0	3 ± 1.12	0	1 ± 0.30
Trifolium pratense	1 ± 0.72	0	0	0
Weeds	9 ± 1.24	0	0	0
Wheat	0	0	0	1 ± 0.30

VI. ii Mean percentage ground cover ± one standard error in the natural regeneration treatments in the summers of 1994, 1995, 1996 & 1997

Species	Year			
	1994	1995	1996	1997
Agrostis stolonifera	2 ± 1.39	0	0	0
Alopecurus geniculatus	0	2 ± 1.16	0	0
Alopecurus myosuroides	0	0	0.1 ± 0.10	1 ± 0.37
Anthemis cotula	0	0	0.4 ± 0.40	1 ± 0.56
Arrhenatherum elatius	0	0	0.3 ± 0.30	0.3 ± 0.30
Avena fatua	4 ± 1.02	3 ± 0.91	0.3 ± 0.17	2 ± 0.69
Bare ground	23 ± 1.87	6 ± 1.64	10 ± 2.27	1± 0.51
Brassica napus	0	0	0	0.3 ± 0.30
Cerastium sp.	0	0	0.3 ± 0.17	0
Cirsium arvense	0	0	0	7 ± 3.02
Cirsium palustre	0	0	1 ± 0.30	0
Cirsium vulgare	0	2 ± 1.30	2 ± 0.96	0
Cynosurus cristatus	0	0.3 ± 0.30	0	0
Dactylis glomerata	1 ± 1.00	0.3 ± 0.30	0	4 ± 1.65
Elytrigia repens	1 ± 0.46	4 ± 1.04	1 ± 0.72	42 ± 5.88
Anisantha sterilis	0	0	0	2 ± 1.17
Festuca rubra	1 ± 0.45	2 ± 1.04	24 ± 4.32	15 ± 3.58
Festuca sp.	0	0.3 ± 0.30	2 ± 2.00	0
Geranium dissectum	0	0	0.3 ± 0.26	0
Holcus lanatus	0	1 ± 0.55	0.03 ± 0.03	1 ± 0.57
Hordeum sp.	0	0.3 ± 0.30	0	0
Lactuca serriola	0	0	0	0.1 ± 0.10
Lolium multiflorum	2 ± 0.76	1 ± 0.52	0	0
Lolium perenne	8 ± 2.80	18 ± 5.18	0	0
Lolium sp.	0	0	34 ± 5.19	1 ± 1.00
Lolium x *boucheanum*	6 ± 2.26	0	0	0
Myosotis arvensis	0	0	0	1 ± 1.00
Pastinaca sativa	0	0	0	1 ± 0.25
Phleum pratense	0.3 ± 0.30	0.4 ± 0.40	0.4 ± 0.40	3 ± 1.66
Poa annua	5 ± 0.83	5 ± 1.89	0	0
Poa trivialis	0	37 ± 5.10	6 ± 2.33	0.3 ± 0.30
Ranunculus repens	0	12 ± 3.66	14 ± 4.54	16 ± 4.99
Rumex obtusifolius	0	2 ± 1.51	0	3 ± 1.00
Senecio vulgaris	0	0	0	0.2 ± 0.13
Sinapis arvensis	31 ± 4.31	0.4 ± 0.28	0.03 ± 0.03	0
Sonchus oleraceus	0	1 ± 0.41	0	0
Taraxacum officinale	0	0	0.1 ± 0.10	0
Trifolium pratense	0.1 ± 0.10	0.1 ± 0.1	0	0
Triticale	0	0	0.1 ± 0.10	0
Weeds	10 ± 1.93	0	0	0

VI. iii Mean percentage ground cover ± one standard error in the *Arrhenatherum elatius* treatments in the summers of 1994, 1995, 1996 & 1997

Species	Year			
	1994	1995	1996	1997
Arrhenatherum elatius	49 ± 3.55	68 ±3.71	80 ± 4.76	92 ± 1.55
Avena fatua	8 ± 1.53	3 ± 0.86	0	1 ± 0.32
Bare ground	19 ± 2.26	10 ± 2.12	12 ± 2.91	5 ± 1.33
Cerastium sp.	0	0	0.1 ± 0.06	0
Cirsium arvense	0	0	0	0.1 ± 0.10
Cirsium vulgare	0	0.1 ± 0.10	0.2 ± 0.13	0
Elytrigia repens	0	0.3 ± 0.26	0	1 ± 0.24
Festuca rubra	1 ± 0.50	0	7 ± 4.19	1 ± 0.35
Festuca sp.	0	0.3 ± 0.30	0	0
Holcus lanatus	0	0.3 ± 0.30	0	0
Lolium multiflorum	1 ± 0.46	0	0	0
Lolium perenne	5 ± 1.93	4 ± 2.58	0	0
Lolium x *boucheanum*	1 ± 1.00	0	0	0
Poa annua	2 ± 0.48	0	0	0
Poa trivialis	7 ± 1.48	9 ± 2.42	0.10 ± 0.10	0
Ranunculus repens	0	3 ± 1.57	0.4 ± 0.28	0
Rumex obtusifolius	0	0	0.1 ± 0.10	0.1 ± 0.10
Senecio vulgaris	0	0	0	1 ± 0.54
Sinapis arvensis	5 ± 0.62	0	0.4 ± 0.38	0
Sonchus oleraceus	0	1 ± 0.36	0.3 ± 0.14	0
Taraxacum officinale	0	0	0	1 ± 1.00
Weeds	5 ± 0.83	0	0	0

VI. iv Mean percentage ground cover ± one standard error in the *Dactylis glomerata* treatments in the summers 1994, 1995, 1996 & 1997

Species	Year			
	1994	1995	1996	1997
Agrostis stolonifera	1 ± 0.42	0	0	0
Anthemis cotula	0	0	0	1 ± 0.76
Avena fatua	6 ± 0.79	4 ± 1.73	0	4 ± 1.35
Bare ground	24 ± 2.32	4 ± 0.98	10 ± 2.52	1 ± 0.55
Cerastium sp.	0	0	1 ± 0.32	0
Cirsium arvense	0	0	0	1 ± 0.24
Cirsium vulgare	0	0	0.3 ± 0.26	0
Dactylis glomerata	27 ± 2.83	50 ± 5.98	79 ± 3.86	74 ± 4.08
Elytrigia repens	2 ± 0.94	0.3 ± 0.30	0	13 ± 3.70
Festuca rubra	0	0	1 ± 0.38	0.4 ± 0.28
Galium aparine	0	0	0	0.1 ± 0.35
Geranium dissectum	0	0	0	1 ± 0.77
Holcus lanatus	0	0	0.1 ± 0.10	0
Hordeum sp.	0	0.3 ± 0.17	0	0
Lolium multiflorum	1 ± 1.00	0	0	0
Lolium perenne	3 ± 1.21	3 ± 1.00	0	0
Poa annua	4 ± 0.86	1 ± 0.52	0	0
Poa trivialis	9 ± 1.44	17 ± 2.88	2 ± 0.81	0
Ranunculus repens	0	22 ± 4.90	7 ± 2.73	3 ± 1.44
Senecio vulgaris	0	0	0	0.4 ± 0.21
Sinapis arvensis	14 ± 2.72	0.1 ± 0.10	0	0
Sonchus oleraceus	0	0.3 ± 0.30	0	0
Trifolium pratense	0.3 ± 0.30	0	0	0
Weeds	6 ± 1.22	0	0	0

VI. v Mean percentage ground cover ± one standard error in the *Festuca rubra* treatments in the summers of 1994, 1995, 1996 & 1997

Species	Year			
	1994	1995	1996	1997
Agrostis stolonifera	0.3 ± 0.30	0	0	0
Alopecurus geniculatus	0	2 ± 1.66	0	0
Alopecurus myosuroides	0	0	2 ± 1.93	0.03 ± 0.03
Alopecurus sp.	1 ± 0.67	0	0	0
Anthemis cotula	0	0	0.1 ± 0.03	1 ± 1.00
Arrhenatherum elatius	0	0	0	1 ± 0.35
Avena fatua	6 ± 0.98	6 ± 1.63	0	2 ± 0.80
Bare ground	25 ± 2.66	6 ± 1.68	4 ± 1.58	0.4 ± 0.28
Brassica napus	0	0	0	0.3 ± 0.17
Cerastium sp.	0	0	0.03 ± 0.03	0
Cirsium arvense	0	0	0	1 ± 0.71
Cirsium palustre	0	0	2 ± 1.29	0
Cirsium vulgare	0	0	1 ± 0.30	1 ± 0.30
Dactylis glomerata	0	0	0	4 ± 2.02
Elytrigia repens	0	5 ± 1.93	10 ± 3.14	5 ± 1.44
Festuca rubra	16 ± 2.17	27 ± 3.94	63 ± 4.67	76 ± 4.02
Hordeum sp.	0	0.3 ± 0.18	0	0
Lolium multiflorum	2 ± 0.94	0	0	0
Lolium perenne	11 ± 3.74	23 ± 6.24	0	0
Lolium sp.	0	0	14 ± 4.27	0
Lolium x *boucheanum*	2 ± 1.58	0	0	0
Lotus corniculatus	0	0	0	1 ± 1.00
Pastinaca sativa	0	0	0	0.1 ± 0.10
Poa annua	4 ± 0.94	2 ± 0.82	0	0
Poa trivialis	6 ± 1.64	18 ± 3.15	0.3 ± 0.30	3 ± 2.13
Ranunculus repens	0	9 ± 3.37	2 ± 1.10	6 ± 2.37
Rumex obtusifolius	0	1 ± 0.51	0.2 ± 0.14	0.1 ± 0.10
Senecio vulgaris	0	0	0	0.3 ± 0.17
Sinapis arvensis	17 ± 2.60	1 ± 0.34	0	0
Sonchus oleraceus	0	1 ± 0.39	0	0
Taraxacum officinale	0	0	0.03 ± 0.03	0
Trifolium pratense	0	1 ± 0.51	0	0
Triticale	0	0	0	0.1 ± 0.10
Weeds	10 ± 2.26	0	0	0
Wheat	0	0	0	0.03 ± 0.03

VI. vi Mean percentage ground cover ± one standard error in the *Phleum pratense* treatments in the summers 1994, 1995, 1996 & 1997

Species	Year			
	1994	1995	1996	1997
Agrostis stolonifera	0	0	0	2 ± 0.82
Alopecurus myosuroides	0	3 ± 1.73	0	0.1 ± 0.10
Anthemis cotula	0	0	0.03 ± 0.03	0
Arrhenatherum elatius	0	1 ± 0.52	1± 0.41	1 ± 0.42
Avena fatua	8 ± 1.45	2 ± 0.73	0.1± 0.10	1 ± 0.30
Bare ground	26 ± 2.73	3 ± 0.80	7 ± 1.73	3 ± 0.99
Brassica napus	0	0	0	1 ± 0.57
Cirsium arvense	0	0	0	0.4 ± 0.28
Cirsium vulgare	0	0	2 ± 1.27	0
Dactylis glomerata	0	0.1 ± 0.10	0.1 ± 0.10	0
Elytrigia repens	0	1 ± 0.46	0.1 ± 0.42	12 ± 3.47
Festuca sp. a	0	0	0.1 ± 0.10	0
Festuca rubra	0	0.1 ± 0.10	1 ± 0.47	2 ± 0.94
Festuca sp. b	0	0	0.03 ± 0.03	0
Galium aparine	0	0	0.1 ± 0.10	0
Geranium dissectum	0	0	0.3 ± 0.30	0
Geranium sp.	0	0	0	1 ± 0.45
Lolium multiflorum	7 ± 3.03	0	0	0
Lolium perenne	4 ± 1.61	7 ± 2.28	0	0
Lolium sp.	0	0	2 ± 1.34	0
Lolium x *boucheanum*	3 ± 2.37	0	0	0
Phleum pratense	24 ± 3.46	63 ± 4.63	76 ± 4.31	71 ± 3.71
Poa annua	2 ± 0.64	2 ± 1.30	0	0
Poa trivialis	0	8 ± 1.84	2 ± 0.84	0.1 ± 0.10
Polygonum aviculare	0	0	0	0.1 ± 0.10
Ranunculus repens	0	9 ± 3.56	6 ± 2.92	2 ± 0.99
Senecio vulgaris	0	0	0	0.3 ± 0.17
Sinapis arvensis	11 ± 1.25	1 ± 0.23	1 ± 0.43	0
Sonchus oleraceus	0	2 ± 0.60	1 ± 0.46	1 ± 0.32
Trifolium pratense	0.2 ± 0.2	0	0	0
Weeds	6 ± 1.03	0	0	0
Wheat	0	0	0	0.3 ± 0.30

VI.vii Mean visimeter recordings ± one standard error for the five grass treatments and the natural regeneration treatments in the winter of 1997

Height category (cm)	Percentage vertical cover ± one standard error					
	Arrhenatherum elatius	*Cynosurus cristatus*	*Dactylis glomeratas*	*Festuca rubra*	Natural regeneration	*Phleum pratense*
0-5	97 ± 1.64	63 ± 4.36	97 ± 1.49	48 ± 4.89	54 ± 4.46	95 ± 1.73
5-10	91 ± 2.85	36 ± 4.70	86 ± 3.14	29 ± 4.74	20 ± 3.70	84 ± 3.53
10-20	71 ± 4.37	18 ± 3.27	58 ± 4.63	16 ± 3.82	9 ± 2.17	53 ± 4.66
20-30	45 ± 4.57	9 ± 2.16	32 ± 4.18	8 ± 2.60	4 ± 1.33	33 ± 4.14
30-40	24 ± 3.83	5 ± 1.24	16 ± 3.04	4 ± 1.79	3 ± 1.12	15 ± 2.54
40-50	15 ± 3.45	1 ± 0.49	8 ± 1.81	2 ± 0.88	2 ± 0.93	7 ± 1.58
50-60	7 ± 2.46	0.4 ± 0.26	4 ± 1.27	1 ± 0.52	2 ± 0.93	4 ± 1.22
60-70	4 ± 1.38	0.1 ± 0.09	2 ± 0.77	0.2 ± 0.09	1 ± 0.75	3 ± 1.09
70-80	2 ± 0.77	0.1 ± 0.1	2 ± 0.47	0.04 ± 0.02	1 ± 0.33	2 0.86
80-90	1± 0.43	0.1 ± 0.1	1 ± 0.46	0.03 ± 0.02	1 ± 0.40	1 ± 0.30
90-100	0.3 ± 0.15	0.1 ± 0.1	1 ± 0.44	0.03 ± 0.02	0.3 ± 0.16	0.1 ± 0.07

VI. viii Mean percentage ground cover ± one standard error of the natural regeneration soil cores between the winters 1994 & 1997

Species	Years			
	1994	1995	1996	1997
Avena fatua	0	17 ± 11.24	0	0
Bare ground	29 ± 7.02	0.2 ± 0.20	5 ± 4.13	0
Dactylis glomerata	1 ± 1.00	0	0	10 ± 6.88
Elytrigia repens	8 ± 8.00	17 ± 11.12	50 ± 14.83	25 ± 9.93
Anisantha sterilis	0	3 ± 3.00	0	0
Festuca rubra	0	6 ± 5.82	33 ± 10.81	40 ± 11.24
Geranium dissectum	7 ± 7.00	0	0	0
Litter	6 ± 4.49	0.2 ± 0.20	0	0
Lolium multiflorum	4 ± 4.00	0	0	0
Lolium perenne	5 ± 5.00	16 ± 11.01	0	0
Lolium x *boucheanum*	3 ± 3.00	0	0	0
Moss	0	0.2 ± 0.20	0	0
Poa annua	4 ± 4.00	0	0	0
Poa trivalis	22 ± 9.84	33 ± 14.14	0	4 ± 2.66
Polygonum aviculare	4 ± 4.00	0	0	0
Ranunculus repens	0	8 ± 8.00	13 ± 6.53	21 ± 8.61
Sinapis arvensis	6 ± 2.23	0	0	0

APPENDIX VII

The influence of beetle banks on cereal aphid predation in winter wheat

Contents:

VII. i Mean number (± one standard error) of aphids in the enclosures (E) and controls (C) on each sampling date on the marked ears of wheat in the year 1996

E/C	2 July	5 July	9 July	12 July	16 July	19 July	23 July
E	1 ±0.26	0.4 ± 0.12	0.2 ± 0.05	0.2 ± 0.05	0.4 ± 0.10	0.4 ± 0.11	2 ± 0.21
C	1 ± 0.14	0.3 ± 0.06	0.1 ± 0.03	0.1 ± 0.03	0.2 ± 0.06	0.2 ± 0.04	1 ± 0.22

E/C	25 July	30 July	2 August	6 August	9 August	13 August	16 August
E	3 ± 0.34	6 ± 0.55	7 ± 0.86	14 ± 11.82	10 ± 1.47	3 ± 0.83	0.3 ± 0.26
C	3 ± 0.40	5 ± 0.80	7 ± 0.97	12 ± 1.95	10 ± 1.71	4 ± 1.04	0.4 ± 0.15

VII. ii Mean number (± one standard error) of aphids in the enclosures (E) and controls (C) on each sampling date on the marked leaves of wheat in the year 1996

E/C	2 July	5 July	9 July	12 July	16 July	19 July	23 July
E	0.1 ± 0.05	0.04 ± 0.01	0.1 ± 0.04	0.1 ± 0.03	0.1 ± 0.05	0.2 ± 0.06	0.7 ± 0.20
C	0.2 ± 0.05	0.1 ± 0.02	0.03 ± 0.03	0.003 ± 0.003	0.1 ± 0.04	0.1 ± 0.06	0.5 ± 0.16

E/C	25 July	30 July	2 August	6 August	9 August	13 August	16 August
E	0.4 ± 0.10	0.3 ± 0.06	1 ± 0.14	2 ± 0.82	3 ± 0.96	8 ± 2.61	1 ± 0.29
C	0.3 ± 0.10	0.5 ± 0.13	1 ± 0.14	2 ± 0.32	5 ± 1.55	7 ± 1.81	1 ± 0.72

VII.iii Mean number (± one standard error) of aphids in the enclosures (E) and controls (C) on each sampling date on the unmarked ears of wheat in the year 1996

E/C	25 July	31 July	6 August	12 August	19 August
E	18 ± 2.33	21 ± 2.11	26 ± 2.72	9 ± 0.99	0
C	17 ± 1.63	17 ± 2.54	17 ± 3.00	4 ± 0.81	0

VII. iv Mean number (± one standard error) of aphids per transect on the marked leaves of wheat, on each sampling date in the year 1996

Transect	2 July	5 July	9 July	12 July	16 July	19 July	23 July
1 (8m)	0.1 ± 0.06	0.07 ± 0.04	0	0.02 ± 0.02	0.1 ± 0.09	0.2 ± 0.01	0.2 ± 0.08
2 (33m)	0.2 ± 0.09	0.02 ± 0.01	0.2 ± 0.09	0.1 ± 0.06	0.2 ± 0.08	0.1 ± 0.07	0.8 ± 0.37
3 (58m)	0.08 ± 0.05	0.02 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.06 ± 0.04	0.1 ± 0.06	0.5 ± 0.17
4 (83m)	0.2 ± 0.08	0.08 ± 0.03	0.05 ± 0.04	0.01 ± 0.01	0.06 ± 0.04	0.2 ± 0.11	0.8 ± 0.28

Transect	25 July	30 July	2 August	6 August	9 August	13 August	16 August
1 (8m)	0.4 ± 0.15	0.5 ± 0.19	0.6 ± 0.16	1 ± 0.15	2 ± 0.82	2 ± 1.02	0.29 ± 0.15
2 (33m)	0.3 ± 0.15	0.4 ± 0.18	0.4 ± 0.14	1 ± 0.35	2 ± 0.77	5 ± 1.48	0.92 ± 0.58
3 (58m)	0.3 ± 0.19	0.2 ± 0.07	0.3 ± 0.07	1 ± 0.50	6 ± 2.21	11 ± 4.14	2 ± 1.37
4 (83m)	0.4 ± 0.09	0.6 ± 0.10	1 ± 0.15	4 ± 1.44	7 ± 2.48	10 ± 3.92	0.96 ± 0.56

VII. v Mean number (± one standard error) of aphids per transect on the unmarked ears of wheat, on each sampling date in the year 1996

Transect	25 July	31 July	6 August	12 August	19 August
1 (8m)	12 ± 1.96	16 ± 9.34	15 ± 3.62	4 ± 1.22	0
2 (33m)	24 ± 2.05	18 ± 3.63	19 ± 5.05	8 ± 1.76	0
3 (58m)	17 ± 3.26	19 ± 3.57	21 ± 3.73	6 ± 1.77	0
4 (83m)	17 ± 2.67	21 ± 2.41	32 ± 2.33	6 ± 1.12	0

VII. vi Mean numbers (± one standard error) of predator taxa caught in pitfall traps in the enclosures (E) and controls (C) on each sampling date in the year 1996

Taxon		16 April	30 April	8 May	15 May	22 May	29 May	5 June
Carabidae	E	3 ± 0.61	1 ± 0.26	1 ± 0.22	0.4 ± 0.18	1 ± 0.27	3 ± 1.31	1 ± 0.34
	C	11 ± 2.16	6 ± 1.13	1 ± 0.27	1 ± 0.29	3 ± 0.78	3 ± 0.80	3 ± 0.56
'Boundary' type carabids	E	2 ± 0.45	1 ± 0.26	0.3 ± 0.14	0.1 ± 0.09	1 ± 0.18	2 ± 0.95	1 ± 0.29
	C	7 ± 1.77	3 ± 0.85	1 ± 0.22	0.4 ± 0.27	1 ± 0.34	2 ± 0.58	2 ± 0.41
'Open-field' type carabids	E	1 ± 0.27	0.4 ± 0.16	0.3 ± 0.15	0.3 ± 0.15	1 ± 0.18	1 ± 0.50	0.4 ± 0.18
	C	3 ± 0.56	3 ± 0.52	1 ± 0.22	0.4 ± 0.13	2 ± 0.52	1 ± 0.35	0.3 ± 0.15
'Highly ranked boundary carabids'	E	0	0.1 ± 0.1	0	0	0.1 ± 0.10	0.6 ± 0.35	0.3 ± 0.15
	C	0.4 ± 0.15	0.3 ± 0.12	0.2 ± 0.10	0.1 ± 0.1	0.1 ± 0.09	0.8 ± 0.31	1 ± 0.28
Bembidion spp.	E	2 ± 0.44	0.4 ± 0.2	0.3 ± 0.14	0.2 ± 0.10	1 ± 0.24	1 ± 0.56	0.3 ± 0.09
	C	8 ± 1.90	3 ± 0.76	0.3 ± 0.20	1 ± 0.22	2 ± 0.65	1 ± 0.39	1 ± 0.34
Trechus quadristriatus	E	0.1 ± 0.09	0.1 ± 0.09	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.10	0.3 ± 0.44	0
	C	1 ± 0.23	1 ± 0.28	0.1 ± 0.09	0.1 ± 0.09	1 ± 0.25	1 ± 0.22	0.3 ± 0.15
Pterostichus melanarius	E	1 ± 0.24	0.3 ± 0.11	0.3 ± 0.14	0.1 ± 0.09	0.3 ± 0.11	1 ± 0.24	0.3 ± 0.15
	C	1 ± 0.39	2 ± 0.26	0.3 ± 0.20	0.1 ± 0.09	0	0.3 ± 0.15	0
Staphylinidae	E	2 ± 0.30	1 ± 0.89	4 ± 0.96	3 ± 1.65	7 ± 1.64	5 ± 1.13	17 ± 3.66
	C	3 ± 0.49	4 ± 1.00	8 ± 1.19	3 ± 1.18	15 ± 4.63	10 ± 3.05	43 ± 10.95
Tachyporus spp.	E	0.1 ± 0.09	1 ± 0.20	3 ± 0.95	3 ± 1.60	6 ± 1.46	3 ± 0.95	12 ± 3.30
	C	1 ± 0.27	3 ± 0.79	7 ± 1.06	3 ± 1.14	12 ± 3.77	7 ± 2.78	36 ± 10.39
Aleocharinae	E	1 ± 0.23	0.4 ± 0.16	1 ± 0.22	0.1 ± 0.10	1 ± 0.22	1 ± 0.27	4 ± 0.53
	C	1 ± 0.29	1 ± 0.16	1 ± 0.11	0.1 ± 0.09	1 ± 0.48	1 ± 0.48	4 ± 1.12
Araneae	E	4 ± 0.60	3 ± 0.59	1 ± 0.32	1 ± 0.30	1 ± 0.46	1 ± 0.26	2 ± 0.25
	C	7 ± 1.06	8 ± 1.07	3 ± 0.63	1 ± 0.27	3 ± 0.46	1 ± 0.29	3 ± 0.74
Linyphiidae	E	4 ± 0.56	3 ± 0.59	1 ± 0.32	0.4 ± 0.18	1 ± 0.39	1 ± 0.26	2 ± 0.25
	C	6 ± 1.04	7 ± 1.01	2 ± 0.57	1 ± 0.22	2 ± 0.46	1 ± 0.25	3 ± 0.72
Lycosidae	E	0.3 ± 0.19	0.1 ± 0.1	0	0.2 ± 0.20	0.1 ± 0.09	0	0
	C	1 ± 0.20	1 ± 0.20	0.4 ± 0.18	0.2 ± 0.14	0.1 ± 0.10	0.1 ± 0.09	0.1 ± 0.10
Total polyphagous	E	9 ± 1.08	5 ± 0.76	5 ± 1.16	4 ± 1.85	9 ± 1.86	9 ± 2.35	35 ± 7.39
	C	21 ± 3.05	18 ± 2.38	12 ± 1.57	5 ± 1.45	20 ± 4.72	14 ± 3.68	89 ± 20.05

Taxon		12 June	19 June	26 June	3 July	17 July	24 July	31 July	7 Augu
Carabidae	E	0.4 ± 0.22	1 ± 0.27	2 ± 0.48	4 ± 1.08	23 ± 4.13	16 ± 3.45	13 ± 2.68	9 ± 0.9
	C	1 ± 0.27	2 ± 0.58	4 ± 0.89	5 ± 1.22	39 ± 8.11	18 ± 2.54	16 ± 3.06	13 ± 1.9
'Boundary' type carabids	E	0.3 ± 0.15	0.3 ± 0.15	1 ± 0.38	1 ± 0.32	1 ± 0.26	1 ± 0.26	2 ± 0.69	0.1 + (
	C	1 ± 0.22	1 ± 0.35	2 ± 0.58	2 ± 0.62	1 ± 0.30	3 ± 0.72	2 ± 0.51	1 ± 0.4
'Open-field' type carabids	E	0	0.3 ± 0.18	1 ± 0.22	3 ± 0.94	22 ± 4.15	15 ± 3.41	11 ± 2.55	9 ± 0.9
	C	0.3 ± 0.15	0.4 ± 0.16	1 ± 0.35	3 ± 0.72	38 ± 7.99	15 ± 2.18	15 ± 2.85	12 ± 1.7
'Highly ranked boundary	E	0.1 ± 0.09	0.1 ± 0.10	0.2 ± 0.10	0.2 ± 0.20	0	0	0	0
	C	0.3 ± 0.14	0.6 ± 0.22	0.8 ± 0.28	0	0	0	0	0.1 ± (
Bembidion spp.	E	0.1 ± 0.09	0.3 ± 0.14	0.2 ± 0.10	0.6 ± 0.24	0.3 ± 0.14	0	0.3 ± 0.14	0
	C	0.4 ± 0.15	0.4 ± 0.14	1 ± 0.27	1 ± 0.27	1 ± 0.16	0.1 ± 0.09	0.1 ± 0.10	0.1 ± (
Trechus quadristriatus	E	0	0.1 ± 0.10	0	1 ± 0.87	17 ± 3.75	13 ± 3.18	9 ± 2.39	1 ± 0.2
	C	0.1 ± 0.09	0.2 ± 0.10	0.1 ± 0.09	2 ± 0.65	31 ± 7.44	14 ± 1.94	12 ± 2.70	2 ± 0.4
Pterostichus melanarius	E	0	0.1 ± 0.09	0.5 ± 0.22	2 ± 0.55	5 ± 0.98	2 ± 0.45	2 ± 0.41	8 ± 1.0
	C	0.2 ± 0.10	0.1 ± 0.07	0.6 ± 0.30	1 ± 0.30	6 ± 1.61	2 ± 0.47	3 ± 0.51	10 ± 1.7
Staphylinidae	E	7 ± 1.17	9 ± 1.47	6 ± 1.48	7 ± 1.81	5 ± 0.83	2 ± 0.83	3 ± 0.74	3 ± 0.5
	C	10 ± 1.63	10 ± 2.32	11 ± 2.34	6 ± 1.18	11 ± 2.02	4 ± 0.73	4 ± 1.14	4 ± 0.3
Tachyporus spp.	E	4 ± 0.78	5 ± 1.05	4 ± 1.24	4 ± 1.61	0.8 ± 0.25	0.3 ± 0.14	0.3 ± 0.14	0.4 ± (
	C	7 ± 1.54	7 ± 2.30	6 ± 1.49	4 ± 1.10	1 ± 0.42	0.6 ± 0.30	0.4 ± 0.15	1 ± 0.2
Aleocharinae	E	2 ± 0.47	2 ± 0.48	1 ± 0.31	2 ± 0.37	3 ± 0.72	1 ± 0.34	2 ± 0.68	2 ± 0.4
	C	2 ± 0.49	2 ± 0.36	3 ± 0.68	1 ± 0.30	6 ± 1.36	2 ± 0.37	4 ± 0.86	3 ± 0.3
Araneae	E	1 ± 0.32	2 ± 0.62	2 ± 0.79	2 ± 0.68	6 ± 0.93	12 ± 1.56	16 ± 1.74	25 ± 1.9
	C	1 ± 0.39	2 ± 0.57	4 ± 0.55	4 ± 0.70	6 ± 0.85	11 ± 1.46	17 ± 1.76	33 ± 2.9
Linyphiidae	E	1 ± 0.30	2 ± 0.63	2 ± 0.80	2 ± 0.68	6 ± 0.93	12 ± 1.56	16 ± 1.71	24 ± 2.0
	C	1 ± 0.38	2 ± 0.57	4 ± 0.52	4 ± 0.66	6 ± 0.81	11 ± 1.48	17 ± 1.75	33 ± 2.9
Lycosidae	E	0.1 ± 0.09	0.1 ± 0.10	0.1 ± 0.10	0	0	0.2 ± 0.14	0.1 ± 0.10	0.2 ± (
	C	0.1 ± 0.10	0	0.1 ± 0.10	0.1 ± 0.09	0.1 ± 0.10	0.1 ± 0.10	0.1 ± 0.10	0.1 ± (
Total polyphagous predators	E	14 ± 2.36	11 ± 1.84	14 ± 3.14	18 ± 4.42	32 ± 5.02	21 ± 3.43	32 ± 4.34	36 ± 2.4
	C	20 ± 3.27	14 ± 2.71	27 ± 5.09	17 ± 2.92	61 ± 10.49	26 ± 3.36	38 ± 4.50	51 ± 3.5

VII. vii Mean number (± one standard error) of predator taxa caught in the D-vac suction samples, in the enclosures (E) and controls (C) on each sampling date in the year 1996

Taxon		16 April	30 April	8 May	15 May	22 May	29 May	5 June	12 June
Carabidae	E	0.3 ± 0.12	1 ± 0.26	0.3 ± 0.19	0.4 ± 0.20	0	0.3 ± 0.14	0.2 ± 0.10	0.2 ± 0.10
	C	1 ± 0.26	1 ± 0.24	1 ± 0.24	1 ± 0.27	0	0.1 ± 0.10	0.1 ± 0.10	0.2 ± 0.14
'Boundary' type carabids	E	0.2 ± 0.10	0.4 ± 0.15	0.2 ± 0.20	0.3 ± 0.12	0	0.1 ± 0.09	0.2 ± 0.10	0.2 ± 0.20
	C	0.3 ± 0.14	0.3 ± 0.15	0.4 ± 0.13	1 ± 0.22	0	0.1 ± 0.10	0.1 ± 0.10	0.2 ± 0.14
'Open-field' type carabids	E	0.1 ± 0.09	0.4 ± 0.18	0.1 ± 0.10	0.1 ± 0.10	0	0.1 ± 0.09	0	0
	C	0.3 ± 0.20	0.3 ± 0.12	0.4 ± 0.15	0.2 ± 0.10	0	0	0	0
'Highly ranked boundary carabids'	E	0	0.04 ± 0.04	0	0.2 ± 0.08	0	0.04 ± 0.04	0.1 ± 0.07	0.1 ± 0.07
	C	0	0	0.09 ± 0.06	0.3 ± 0.11	0	0.04 ± 0.04	0.04 ± 0.04	0.1 ± 0.08
Bembidion spp	E	0.3 ± 0.11	1 ± 0.26	0.2 ± 0.20	0.2 ± 0.14	0	0	0	0
	C	1 ± 0.22	1 ± 0.22	1 ± 0.20	0.3 ± 0.14	0	0	0	0
Staphylinidae	E	3 ± 0.68	3 ± 0.74	4 ± 0.72	3 ± 0.58	0.2 ± 0.10	0.4 ± 0.26	0.1 ± 0.10	0
	C	5 ± 0.48	5 ± 0.82	5 ± 0.81	2 ± 0.76	0.2 ± 0.14	0.1 ± 0.10	0	0.1 ± 0.09
Tachyporus spp	E	1 ± 0.29	1 ± 0.30	1 ± 0.15	1 ± 0.27	0	0.1 ± 0.10	0	0
	C	1 ± 0.40	2 ± 0.39	2 ± 0.41	1 ± 0.29	0.1 ± 0.09	0.1 ± 0.10	0	0
Aleocharinae	E	2 ± 0.45	2 ± 0.52	3 ± 0.60	2 ± 0.48	0.1 ± 0.09	0.3 ± 0.15	0	0
	C	2 ± 0.32	3 ± 0.63	3 ± 0.55	1 ± 0.47	0.1 ± 0.1	0	0	0
Araneae	E	1 ± 0.22	0.4 ± 0.13	1 ± 0.14	0.4 ± 0.18	1 ± 0.23	0.4 ± 0.15	1 ± 0.20	1 ± 0.18
	C	0.4 ± 0.18	1 ± 0.18	0.3 ± 0.15	0.4 ± 0.20	1 ± 0.18	0.1 ± 0.09	1 ± 0.24	0.3 ± 0.20
Linyphiidae	E	1 ± 0.22	0.4 ± 0.13	1 ± 0.14	0.4 ± 0.18	1 ± 0.23	0.4 ± 0.15	1 ± 0.21	1 ± 0.18
	C	0.4 ± 0.18	1 ± 0.18	0.3 ± 0.15	0.4 ± 0.20	0.4 ± 0.16	0.1 ± 0.09	1 ± 0.26	0.3 ± 0.19
Cantharidae spp	E	0	0	0	0	0.5 ± 0.20	1 ± 0.20	1 ± 0.31	0.1 ± 0.09
	C	0	0	0	0	1 ± 0.24	1 ± 0.27	1 ± 0.23	0.1 ± 0.09
Total polyphagous predators	E	4 ± 0.82	4 ± 0.80	5 ± 0.66	4 ± 0.71	1 ± 0.23	1 ± 0.35	1 ± 0.18	1 ± 0.19
	C	6 ± 0.72	6 ± 0.84	6 ± 1.00	4 ± 0.96	1 ± 0.27	0.3 ± 0.14	1 ± 0.27	1 ± 0.31

APPENDIX VIII

The impact of beetle banks on the dispersal and distribution of polyphagous predators in cereal crops

Contents:

VIII.i Summary description of the five pairs of fields used in the study

VIII.ii Mean percentage ground cover (± one standard error) of the vegetation on the beetle banks. Numbers 1-5 denominate which pair of fields the beetle banks belong to.

VIII.iii Mean percentage ground cover (± one standard error) of the vegetation in the field margins of the fields containing beetle banks. Numbers 1-5 denominate which pair of fields the field margins belong to.

VIII.iv mean percentage ground cover (± one standard error) of the vegetation in the field margins of the fields without beetle banks. Numbers 1-5 denominate which pair of fields the field margins belong to.

VIII.i Summary description of the five pairs of fields with and without beetle banks

Pair	Year beetle bank was created	Width of field from field boundary to either the centre of the field or to the beetle bank (m)	Crop type on experimental side of beetle bank	Crop type on non-experimental side of beetle bank	Location of fields with a beetle bank (Grid reference SK)	Location of fields without a beetle bank (Grid reference SK)
1	August 1993	192	Winter barley	Winter beans	Loddington Estate (SK 799 009)	Parkers Ltd (SK 784 016)
2	November 1993	168	Winter barley	Winter wheat	Loddington Estate (SK 798 014)	Loddington Estate (SK 805 024)
3	September 1992	240	Winter barley	Winter beans	Loddington Estate (SK 797 020)	Parkers Ltd (SK 785 014)
4	September 1993	192	Winter wheat	Winter wheat	Edmonthorpe Estate (SK 840 169)	Parkers Ltd (SK 854 040)
5	September 1993	240	Winter wheat	Winter wheat	Edmonthorpe Estate (SK 843 164)	Parkers Ltd (SK 851 042)

VIII.ii Mean percentage ground cover (± one standard error) of the vegetation on the beetle banks. Numbers 1-5 denominate which pair of fields the beetle banks belong to.

Species	Beetle bank 1	Beetle bank 2	Beetle bank 3	Beetle bank 4	Beetle bank 5
Aethusa cynapium	0	5 ± 3.98	0	0	0
Anthemis cotula	0	0	0	1 ± 1.00	0
Arrhenatherum elatius	0	5	0	0	0
Chrysanthemum leucanthemum	0	5	0	0	0
Cynosurus cristatus	0	0	0	5 ± 4.99	0
Dactylis glomerata	39 ± 8.52	43 ± 12.46	88 ± 3.84	54 ± 8.15	61 ± 12.26
Elytrigia repens	0	0	0	0	1 ± 1.00
Festuca rubra	0	0	0	0.3 ± 0.21	0
Galium aparine	0	0	12 ± 3.82	0	1 ± 1.00
Holcus lanatus	21 ± 7.05	29 ± 10.32	0	21 ± 6.38	12 ± 9.89
Lotus corniculatus	3 ± 2.13	0	0	0	0
Myosotis arvensis	0	6 ± 4.00	0.2 ± 0.20	0	0
Phleum pratense	30 ± 8.71	5 ± 5.00	0	17 ± 5.78	6 ± 4.00
Rumex obtusifolius	0	0	0	1 ± 1.00	4 ± 4.00
Urtica dioica	0	0	0	0	15 ± 9.69

VIII.iii Mean percentage ground cover (± one standard error) of the vegetation in the field margins of the fields containing beetle banks. Numbers 1-5 denominate which pair of fields the field margins belong to.

Species	Field margin 1	Field margin 2	Field margin 3	Field margin 4	Field margin 5
Aethusa cynapium	0	0	0	0	5 ± 2.99
Alopecurus myosuroides	0	0	0	0	1 ± 1.00
Anisantha sterilis	2 ± 1.33	6 ± 2.17	2 ± 1.53	0	15 ± 7.09
Anthemis cotula	0	0	0	0	1 ± 1.00
Arrhenatherum elatius	31 ± 12.15	28 ± 11.06	0	8 ± 5.54	33 ± 9.13
Avena fatua	0	1 ± 1.00	0	0	0
Cirsium spp.	0	0	0	0	5 ± 5.00
Cynosurus cristatus	0	2 ± 1.07	0	0	0
Dactylis glomerata	0	7 ± 7.00	0	4 ± 4.00	2 ± 1.11
Elytrigia repens	58 ± 14.59	36 ± 10.56	88 ± 4.90	52 ± 11.96	10 ± 3.02
Galium aparine	4 ± 2.99	15 ± 6.43	1 ± 1.00	0	11 ± 4.44
Heracleum sphondylium	0	0	0	0	9 ± 6.05
Holcus lanatus	0	0	0	26 ± 10.23	1 ± 1.00
Myosotis arvensis	0	4 ± 4.00	0	0	2 ± 1.31
Papaver sp.	0	0	0	0	3 ± 2.13
Poa trivialis	0	1 ± 1.00	1 ± 1.00	3 ± 3.00	0
Rubus fruticosus	3 ± 3.00	0	0	0	0
Rumex obtusifolius	0	0	0	0	2 ± 1.33
Urtica dioica	3 ± 2.00	3 ± 2.01	7 ± 4.90	0.1 ± 0.10	3 ± 1.34

VIII.iv Mean percentage ground (± one standard error) cover of the vegetation in the field margins of the fields without beetle banks. Numbers 1-5 denominate which pair of fields the field margins belong to.

Species	Field margin 1	Field margin 2	Field margin 3	Field margin 4	Field margin 5
Aethusa cynapium	0	2 ± 2.00	0	0	0
Anisantha sterilis	23 ± 8.89	15 ± 6.30	0	0	1 ± 1.00
Arrhenatherum elatius	44 ± 13.38	4 ± 4.00	54 ± 13.66	17 ± 9.46	25 ± 9.89
Cirsium sp.	0	0	0	8 ± 5.93	0
Dactylis glomerata	12 ± 9.21	0	21 ± 10.53	13 ± 9.64	14 ± 6.99
Elytrigia repens	10 ± 6.85	54 ± 9.13	0	25 ± 8.61	41 ± 8.64
Galium aparine	1 ± 1.00	2 ± 1.11	2 ± 2.00	25 ± 7.90	2 ± 1.07
Holcus lanatus	1 ± 1.00	0	0	1 ± 1.00	0
Lolium perenne	0	0	11 ± 7.47	0	0
Phleum pratense	0	0	7 ± 2.48	0	2 ± 2.00
Poa trivialis	0	0	6 ± 2.08	0	0
Rubus fruticosus	0	0	1 ± 1.00	0	1 ± 1.00
Urtica dioica	10 ± 3.94	25 ± 9.67	0	14 ± 4.27	14 ± 4.35